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THE PROBLEM OF ACQUIRED PHYSIOLOGICAL IMMUNITY IN PLANTS

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I. INTRODUCTION

A KNOWLEDGE of the principles underlying the reactions of a host attacked by a parasite has been of inestimable value in the understanding and control of human diseases. So, too, phytopathology has found that the study of immunity and susceptibility has made possible much of its progress in recent years. Three of the major advances in the present century in plant pathology are closely dependent upon a knowledge of the factors of immunity and susceptibility, namely, the breeding for disease resistance, the discovery of the significance of biological races, and the study of the effect of environment upon plant disease. The ability of the animal to resist infection by the acquirement of a state of partial or complete immunity, contingent upon sensitization by the parasite, is the basis of the most important recent advance in medicine, serotherapy. Accordingly, plant pathologists have not failed to recognize the important theoretical and practical advantages of a knowledge of the rôle of acquired immunity in plants. As early as 1901 Ray and Beauverie offered the first suggestions regarding a display of immunological reactivity in plants comparable to that in animals. Many other plant pathologists, physiologists, and geneticists have since considered this possibility in theory, in observation, and in experiment.

This type of work is comparatively unknown to American investigators which is due, in part at least, to the fact that there has appeared no adequate analysis of this field of study in English. The writer, when questioned regarding acquired immunity in plants has repeatedly been forced to direct his interrogators to the excellent monograph of Carbone and Arnaudi (47), which being in Italian cannot be studied freely by most American botanists. To the intensive student in the field of plant immunity this work is a most valuable contribution, but to the botanist who does not specialize in immunology yet who wishes to be informed upon this subject, the work of Carbone and Arnaudi is usually assimilated with such difficulty

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that it fails to afford the practical answer to the inquiring American botanist.

The problem of acquired immunity in plants is rapidly passing its orientative stage. It is accordingly imperative that our knowledge in this field be reduced to a tangible and assimilable basis which will serve both to stabilize this branch of plant pathology and to guide future investigation in the field. Since the appearance of the monograph of Carbone and Arnaudi several important contributions in acquired plant immunity have lent new viewpoints to the problem, and these tend to modify our conception of the significance and value of the field.

There has been evident a growing tendency for pathologists to attribute observations of various nature to acquired immunity in plants. Unfortunately such points of view are frequently based on no experimental evidence and merely represent analogy. Without any available and adequate critique of the subject to act as a stabilizer of such theory, this tendency to unconstrained comparison has led many botanists to wholly erroneous conclusions regarding the rôle of acquired immunity in plants. The expressions of human serology have been applied to the most heterogeneous plant phenomena *ad libitum* until there is a grave danger that the few really valuable findings in this field may be lost in an inextricable maze of speculation and insufficiently grounded hypothesis. Such erroneous comparisons are rendered particularly confusing by the lack of discrimination in the employment of serological terminology to plant phenomena of obviously distinct nature. The indiscriminate use in plant reactions of such terms as *antigen*, *precipitin reaction*, and *antitoxin* in view of their precise and restricted meanings in serology, leads the average botanist to assume that there is evidence that such phenomena are *homologous* in the two fields, whereas in many cases such "homology" is merely a superficial analogy.

During his investigations in plant immunology the writer has felt it necessary to assemble and survey all of the available work bearing upon this problem. For the reasons outlined above it has been suggested that the results of this survey be made available to American investigators. The present paper is accordingly designed to meet the need for such information by rendering accessible and digestible the mass of accumulated evidence regarding the immunological behavior of plants, analyzing the present status of the subject together with the contentions which have been adequately demonstrated or refuted, and from the results of this analysis indicating the direction of future research in this field.

II. IMMUNOLOGICAL CONCEPTIONS AND TERMINOLOGY

In order to have a basis for a clear understanding of the problem of acquired immunity in plants it is first necessary to understand the various concepts and terms of immunology as they apply to plant phenomena. That a plant may be successfully invaded by a parasite it must possess a greater or less degree of *susceptibility*. The converse of susceptibility, i.e. the ability of a plant to withstand parasitic invasion, is *resistance* or *immunity*. These last two terms, however, have come to have distinct meanings in plant immunology. Fischer and Gäumann (64) very wisely limit the expression *immunity* to phenomena of the type of the reactions of animals to infection, i.e. to the ability of withstanding infection acquired by the host as the result either of stimulation by the parasite or of the introduction of protective substances. *Resistance*, on the other hand, applies to the congenital

capability of a plant to withstand parasitic attack. Resistance and immunity may be of various types. In the first place they vary greatly in degree. Absolute susceptibility, resistance, and immunity are comparatively rare, these properties being relative. We speak of certain grains as being resistant to the wheat rust. Actually the rust mycelium is able to penetrate the tissues of such resistant hosts but is unable to establish a permanent nutritional régime; the host is accordingly not absolutely but practically immune. Susceptibility and resistance or immunity may be generalized through the whole plant body or may be localized in certain tissues. Susceptibility or resistance may extend in duration throughout the life of the plant or may be temporary, at some one stage of development of the host. Both may be profoundly influenced by the environment. Immunity may be specific, directed toward a single type of organism employed in immunization, or may be non-specific or general, directed against a wide range of parasites. Resistance and immunity may be anatomical or morphological in character, or on the other hand they may be of a chemical or physiological nature. Finally, chemical or physiological immunity in the sense defined above may be either passive, static, due to the introduction of protective substances, as in human medicine by the injection of antitoxins, or on the other hand active, dynamic, due to the elaboration by the host of protective substances as a result of stimulation by the parasite, as in the immunity acquired by man as the result of an attack of smallpox.

In order that parasitism be successful the parasite must accomplish three ends: (a) It must penetrate to a suitable infection court; (b) it must establish a satisfactory nutritional régime; and (c) it must resist attempts on the part of the host to restrict or destroy it. Susceptibility depends upon the accomplishment of all these ends. Immunity, in our sense, consists in the breaking of this course at the last point.

The present paper deals with acquired physiological immunity in plants. From the foregoing analysis of the terminology we may now define this expression as the capability of withstanding infection acquired by the host either through the introduction of protective chemical substances of biological origin (passive), or through the elaboration of such protective substances in the host as a result of stimulation by the parasite. While the expressions host and parasite have been used throughout the discussion above, it must be understood that the same principles as apply to the host-parasite relationship apply also to the relation between two symbionts or between a plant and introduced substances of a stimulative nature, such as toxins or proteins which if not counteracted or inactivated would have a deleterious effect upon the plant.

The mechanisms of acquired physiological immunity in animals are the *antibodies*. This term applies to chemical substances of biological origin which have the function of neutralizing or counteracting the introduced protein or other foreign body, which latter stimulating agents are known as *antigens*. The term antibodies is not to be understood as applying to substances of well defined composition, since their nature has never been fully understood in animal serology. Antigens appear to be large colloidal molecules, and are probably chiefly or entirely protein in nature. The antibodies may be *normally* present in the blood of non-immunized animals or they may be present only as the result of stimulation by introduced antigens (*immune antibodies*). The antibodies are demonstrated by a number of types of reaction, although it is not certain as yet whether

these different types of reaction are due to different manifestations of the same antibody or whether different types of antibody are responsible for them.

The major types of reaction are briefly characterized as follows:

1. The *precipitin reaction* is due to the precipitation of a soluble antigen by the antibodies, here called *precipitins*, in the blood of animals immunized against the specific soluble antigen.
2. The *agglutinin reaction* occurs when the antigen is not soluble but in the form of discrete and visible particles, such as bacteria, blood corpuscles, or in plants possibly as plastids or pollen. It is due to the action of antibodies known as *agglutinins* and results in a clumping together of the foreign bodies and the consequent inactivation of the latter.
3. The *toxin-antitoxin reaction* is the neutralization of an introduced poison (*toxin*) by antibodies here known as *antitoxins*. Introduced toxins may be either antigenic (as many bacterial products) or non-antigenic (as certain mineral poisons).
4. *Anaphylaxis* is an immune reaction in which an organism inoculated with an antigen shows violent symptoms of distress upon the introduction of a second, very small dose of the same antigen after an interval of time in which *sensitization* to the antigen has occurred.
5. *Lysis* is the dissolution of non-soluble or soluble antigenic material by antibodies here known as *lysins*. It customarily takes the form of the disintegration and solution of bacteria or corpuscles in the presence of immune serum, and according to the type of antigen broken down may be variously designated as *bacteriolysis*, *hemolysis*, *cytolysis*, *proteolysis*, etc.
6. *Phagocytosis* is a manifestation of immunity in which certain specialized cells of the body (*phagocytes*) are able in an amoeboid fashion to engulf and digest invading organisms, in particular bacteria. It is more a function of congenital than acquired immunity.
7. *Mithridatism* (from Mithradates VI, king of Pontus, who was believed to have so saturated his body with poisons that he was immune to poisoning) or *habituation* is much less truly an immune reaction than the other types of immune reaction listed above, since it is much weaker and less specific than the other reactions. It is exemplified in the tolerance shown by chronic addicts to narcotics and by animals treated with increasing doses of certain non-antigenic poisons, such as arsenic.

This outline, in the preparation of which the writer is particularly indebted to the monograph of Wells upon the chemistry of immune reactions (185), is in brief a statement of the terminology of animal immunity. In animal immunology the customary sequence of events is as follows: An antigen is introduced into the blood system of an animal. This antigen may be soluble, as egg albumen, or particulate, as in the case of foreign blood corpuscles or bacteria, and in the latter cases may be of a virulent strain, producing a severe attack of disease, or a non-virulent or attenuated strain, producing a mild symptomatic display (*vaccination*). After a given period of time during which antibody-formation occurs, the blood of the immunized animal is withdrawn, clarified,

and tested against the antigen (usually with dilution and incubation at 37°C.). Immunity is manifested by a precipitation or cleavage of the antigen if the latter is soluble, by agglutination or lysis of particulate antigens, or by a combination of these reactions. These reactions are usually specific, i.e. positive in high dilution only toward the specific antigen used in the original inoculation. The antibodies are usually characterized by thermolability, activity in very high dilution, dependence upon the presence of electrolytes, and behavior as colloids in regard to electrical fields and dialyzing membranes.

As the result of the production of such antibodies the animal has now become immune in greater or less degree toward the antigen. If the antigen was a poison a large dose no longer exerts the same toxic effect as it would have in the non-immunized animal. If the antigen was a pathogenic organism it is no longer able to produce in the host the same severe pathological effects as it could originally have produced. If the immunity has resulted from an infective attack, the animal either recovers or its symptoms are at least ameliorated. If the antigen was in the form of a vaccine, the host is no longer highly susceptible to virulent attacks of the pathogenic organism. The serological display is hence causatively associated with pathological phenomena and the two types of effects serve to explain each other.

Now from the foregoing analysis it becomes apparent that any application of the zoöimmunitary concepts and terminology to plant phenomena must of necessity involve reactions homologous in the two kingdoms. Every precipitate observed in plant fluids is not a "precipitin reaction," but only such precipitates as are due to *precipitins* in the zoöimmunitary sense, acting in essentially the same fashion as zoöprecipitins; every clumping of bacteria or plastids in plants or plant fluids is not an "agglutination," but only such clumping as is due to the action of *agglutinins* in the sense of serology.

It is certainly not to be understood that all reactions of plants of an immunological nature must necessarily be of the same types as the serological reactions. The differences in gross physiology might well lead to different types of immune reactions in plants and in animals. Thus the inhibition of fungus spore germination or the modification of mycelium *in vivo* have no exact counterpart in serology, yet they doubtless play an important rôle in phytoimmunity. Hence a rigid adherence to serological nomenclature will not only lead to false homologies but will needlessly restrict the terminology of phytoimmunity, and it is accordingly here emphasized that serological nomenclature be applied to plant immunology only where there is definite proof that the reactions described are of the same type, and that it be openly recognized that there may be in plants immunological phenomena having no counterpart in serology due to the gross physiological differences in plants and animals, and that such phenomena demand investigation and discussion as unique plant problems, unhampered by an artificial attempt at homology with zoöimmunitary concepts and terminology.

III. THE DEVELOPMENT OF THE CONCEPTION OF ACQUIRED IMMUNITY IN PLANTS

Having an understanding of the conceptions and terminology of immunology as an aid in discussion of the subject, it is now possible to pass to a consideration of the contributions which have been made in this field. This may best be accomplished first by briefly reviewing in a chronological manner the main steps in the progress of the development of the problem, and then passing to a detailed account of the theories

and findings in the various branches of the field. Accordingly the present section will be devoted to such an account.

The studies in acquired immunity in plants were inaugurated by the reports of Ray (147) and Beauverie (10) in 1901 of successful vaccination of certain plants against fungus diseases. In 1903 Hiltner and Störmer (74) and Süchting (169) advanced the hypothesis that the morphology and behavior of the root tubercle bacilli of Leguminosae are controlled by an acquired immunity of the leguminous symbiont. Two years later Schiff-Giorgini (155) came to the conclusion that the olive tree resists the attack of bacteria in the tubercle disease by the active production of antibodies. Meanwhile Bernard had been carrying on studies on the reasons underlying behavior in mycorrhizae, and in 1909 (16) published a complete account of the display of acquired immunity in the orchid mycorrhiza. Bernard's studies were also continued in subsequent years. Tischler in 1911 (170) suggested that the recovery of *Euphorbia* from a rust disease was due to acquired immunity of host against parasite. Brierley in 1915 (26) believed the same explanation was applicable to recovery of mosaic-diseased tomato plants. The following year Heinricher (71) suggested that pear may acquire an immunity to the mistletoe, *Viscum album*, an observation which he later confirmed in 1929 (72). Similarly Montemartini in 1918 (121) advanced the theory that oak may recover from attacks of the mildew through mechanisms of acquired immunity, an hypothesis which he supported with experimental proof in 1930 (122).

In the same year appeared the first of Magrou's studies on acquired immunity in mycorrhiza (110), the forerunner of several such works by the same investigator. Picado, in 1921 (141) reported the demonstration of acquired and specific agglutinins and lysins in a number of plants, while Lumière and Couturier, also in 1921 (106), believed they had observed anaphylaxis in plants. The work of Lumière and Couturier, however, was contradicted by that of numerous subsequent workers. In 1922 Kořínek (80) was unable to demonstrate antibodies resulting from the injection of saprophytic bacteria into plants. The same year marks the first of Carbone's studies in the field.

The following year negative results were obtained by Carbone (36) in potato inoculations, by Carbone and França (48) in feeding protein to insectivorous plants, and by Brown in connection with crown gall of paris daisy and rose (27). Cappelletti in the same year (29, 30) published the first of his studies dealing with acquired immunity in leguminose root tubercles. Carbone and Arnaudi in 1924 (45) were unable to demonstrate acquired antibodies in *Laurus*, although they made a notable contribution to the study of circulation of antibodies in plants. In 1925 Zoja (192), Hursch (75), Doussain (56), and Arnaudi (4) all reported successful vaccination of plants. Sardiña's results in 1926 (154) pointed to an absence of acquired immunity in a number of plant diseases, as did also those of Riker (152) with crown-gall.

In 1927 appeared the first edition of Nobécourt's excellent monograph upon the subject of acquired immunity in plants (136). He was able to vaccinate successfully, and came to the conclusion that although acquired immunity is present in plants it is customarily restricted to the cell and is not humoral in the sense of serology. Benigni in the same year (12) obtained a temporary immunity following vaccination of corn against smut.

Kostoff's long series of studies, in which numerous manifestations of acquired immunity were believed to result from grafting, tumor formation, hybridization, etc.,

began with a first paper in 1928 (82). The immunological interpretations of this work have been largely or entirely contradicted, however, by the work of Chester and Whitaker (52, 53, 187). Carbone in the same year published an excellent account of vaccination in plants (42) in which he inclined to the view that this phenomenon had been satisfactorily demonstrated. Likewise in 1928 Arnaudi (7) successfully vaccinated pea against *Blepharospora cambivora*.

The monograph in 1930 of Carbone and Arnaudi (47) supplied a working basis for more thorough investigation in this field and offered a comprehensive view of the work of these authors as well as of the numerous earlier investigators.

Finally several contributions of immunological significance have been reported in the past two or three years, of which the more important are East's observations on the recovery of sugar cane from the mosaic disease (60–62) and on the behavior of hybrid embryos in parent tissues (59, 60), Gravatt and Gill's hypothesis that an increased resistance of chestnut to *Endothia* canker may be due to acquired immunity (70), and the work of the school of Carbone furthering the study of antibodies in plants and emphasizing the necessity for distinguishing between true antibodies of the zoöimmunitary type and non-specific "pseudoantibodies."

This very brief chronological sketch having pointed out the main steps in the progress of the conception of acquired immunity in plants, we are now prepared for a more detailed discussion of the results obtained in this field. The following section will accordingly deal with the views, opinions, and *a priori* arguments regarding the possibility of acquired plant immunity, while subsequent sections will be concerned with the actual experimental data thus far obtained.

IV. A PRIORI ANALYSIS OF THE POSSIBILITY OF ACQUIRED IMMUNITY IN PLANTS

Although plants and animals are of presumably common origin they differ markedly in many gross structural and physiological properties. Are these gross differences such as to preclude the possibility of a display of immunological phenomena of the serological type? This is a question which in its various aspects has been considered by many of the investigators of plant immunology, and one which warrants the attention of the present section. The various points for consideration will be: (a) nature of the circulatory system, (b) manner of growth, (c) opportunity for sensitization, and (d) nature of disease and resistance to disease. These points will accordingly be successively considered.

Perhaps the most fundamental objection to an *a priori* belief that plants may elaborate antibodies is the difference of circulatory system between plants and animals in view of the fundamental rôle of the blood in elaborating and distributing immunological bodies. In the mammalian body we have an internal, relatively homogeneous current of high protein content and constant temperature rapidly pervading all parts of the body. An injected substance is soon distributed throughout the whole body and opportunity for sensitization is much more widespread than if the injected substance were localized at the point of original injection. The constant temperature and high protein content afford uniform and favorable conditions for antibody production and demonstration, conditions which certainly do not obtain in the plant body. For in the latter the conventional conception is of an ascending stream of water and mineral salts in the xylem system and a descending stream of elaborated food in aqueous solution in the phloem elements. The two systems are customarily

considered distinct, much less rapid than the blood flow, containing a much lower percentage of protein, and subject to much variation due to environmental variables. The conventional view does not ordinarily consider any appreciable horizontal transfer of elements from these streams nor reversal of flow. If this is the complete and accurate picture of circulation in the plant, then it would appear at first glance that the objections to the hypothesis of acquired antibody formation in the latter have some justification. Such objections, however, are based on three assumptions, namely that the blood stream is essential to antibody production and demonstration in animals, that immunization in animals is necessarily generalized throughout the animal body and not localized, and that the plant circulation differs from the animal circulation in the respects mentioned above. Recent investigations, however, have shown that none of these unreserved assumptions is justified.

That the mammalian blood stream is essential to the production of antibodies in animals has been contradicted by evidence from a number of sources. Thus the production of antibodies has been observed not only in vertebrates but also in many of the invertebrates, in which a blood stream is either lacking or of a type profoundly different from that of mammals. Moreover the studies of Carrel (cited in 173) and his associates have shown that it is possible to demonstrate immunological reactivity of isolated mammalian tissues in artificial culture entirely lacking a blood system. That immunization in animals is necessarily generalized throughout the animal body is refuted by the fact that certain parts of the body may be sensitized and may produce antibodies without this reactivity extending beyond the part inoculated. Thus Besredka (21) in an extended study of this subject shows, for example, that the skin alone of guinea pigs may be immunized to anthrax, that inoculation of *Staphylococcus* into the anterior chamber of the eye leads to immunity of the anterior chamber but of no other part of the body, and that ingestion of the dysentery bacillus by rabbit, mouse, or man is followed by a local immunity in the intestinal wall, the blood being unaffected. Finally the most recent investigations of the circulatory system in plants show it to be far less simple in operation than had been previously believed. Thus there is evidence that translocation in phloem and xylem is not restricted to motion down and up respectively but that reverse currents may occur, while lateral transportation is probably much more frequent than had been suspected. Transport may be relatively much more rapid than had before been believed. For example, East observed (60) in sugar cane that mosaic virus may travel as much as 18″ in 5–7 days. The possibility of circulation in the plant of precipitable animal protein has been demonstrated by Kraus, von Portheim, and Yamanouchi (96) who were able to recover in the plant the reactive constituents of blood serum in a solution of which the plants had been grown. Likewise Arnaudi (47) successfully employed serotherapeutic treatment in crown-gall of geranium by permitting the cut geranium stems to absorb animal antibodies, a process which is based upon the possibility of the circulation of antibodies within the plant organism.

There is very little doubt that it is possible for certain chemical substances at least to be so rapidly and effectively distributed throughout the plant as to function in prophylaxis. A. Müller in his extended treatise on the inner therapy of plants (131) records numerous instances of such effective distribution in the plant body. Wormald and Grubb (189) found that the substances responsible for immu-

nity of apple to crown-gall were circulated through the plant body and transmitted from immune scion to susceptible stock. This same was not true, however, in the case of immunity of potato against *Synchytrium endobioticum* (Roach, 153) nor in that of *Chrysanthemum* rust (Gibson, 68). There is, moreover, an extensive literature dealing with the translocation of various more or less complex chemical substances from one graft symbiont to the other. Evidence of such translocation of glucosides, alkaloids, and proteins is afforded by the experiments of Strasburger and Klinger (atropin), Laurent (atropin), Guignard (alkaloids, cyanohydric glucosides), Gräfe and Lensbauer (nicotin), Mitosch (albumin), Meyer and Timpe (factor controlling variegation), and Baur (virus). There are experiments in which the failure of certain substances to cross the graft union has been recorded, but for the purposes of our argument these positive results definitely indicate that the circulation of numerous complex organic substances including proteins is possible through the graft union, and the deduction necessarily follows that such complex substances are capable of effective circulation in the ungrafted plant.

It is possible to select for studying the circulation of antigenic material plants which are much more favorable than the ordinary flowering plants used. Certain algae and fungi which show rapid plasmatic circulation through large cells or long coenocytic stretches are particularly useful in this regard, *Phytophthora*, *Caulerpa*, *Nitella*, *Valonia*, and *Halocystis* representing a few such cryptogams. Almost nothing has been done in studying immunological reactions in such plants as these. To be sure Prát (142) reports a few experiments with *Caulerpa prolifera* in which he injected dyes and starch and then observed subsequent distribution of the injected substance. He found there was a limited distribution of the color but this was complicated by discoloration *in vivo*, by coagulation of the protoplast, and also doubtless by other traumatic effects since the dyes used (methylene blue, neutral red, Berliner Blau: leicht löslich . . . Grübler) although "vital" in the usual sense of the word undoubtedly exert some toxic effects after a period of observation as long as 2–4 days. In view of the inconclusive results of these experiments, *Caulerpa* and other similar plants could be investigated with profit, first as regards their circulation and proceeding from that to a study of their capability to acquire physiological immunity.

Hence we see that the *a priori* objections against the demonstration of acquired immunity in plants based upon differences in circulation are not as fundamental as first appeared, for not only can the animal show acquired antibody formation independent of the blood circulation, but also the circulation in plants is much more effective in distribution of antigenic material to the cells than had earlier been assumed.

A second difference between plants and animals leading to an *a priori* belief that the zoöimmunitary type of reactions could not play a practical rôle in plant pathology is that of manner of growth. The plant grows in an indeterminate fashion, continually producing new tissues from primary and secondary meristems, while the animal merely grows in size, the whole structure and form being determined from an early stage in development. Hence it might follow either that the plant would be incapable of any but a very transitory acquired immunity because the antibodies would be so diffused and diluted as to lose their importance, pathologically, or that a mechanism for the self perpetuation of the antibodies must be hypothesized.

This argument, it appears to me, is of somewhat greater importance than the

last, but it concerns primarily the practical applications rather than the theoretical demonstration of acquired immunity in plants. We are accustomed to think of acquired animal immunity in terms of long periods of time. Thus the period of protection from smallpox vaccination is customarily stated at seven years, that from typhoid vaccination at three years, etc. On the other hand we have very little evidence regarding the duration of acquired immunity in plants. The few experiments which have considered this point (12, 192) have indicated an acquired immunity in the plants employed of a duration of one to several weeks. This does not, however, preclude the possibility of a more extended period of acquired immunity. Even an acquired immunity of no longer than this serves to establish the theoretical possibility of acquired immunity in plants. Furthermore, a duration no longer than this might have important practical bearings as well, particularly in the cases of the diseases of plants in which the period of susceptibility is relatively limited ("damping-off" of seedlings, rust diseases, bacterial infections of succulent tissues).

Thus we see that the *a priori* argument against the demonstration and practical bearing of acquired immunity in plants based on the continuous, indeterminate growth of plants is interpreted in terms of an inactivation throughout progressive dilution of the immune substance which in turn would tend to limit narrowly the period of immunity. Such being the case, one sees from the foregoing analysis that this argument is of value only from the practical standpoint, not from the theoretical, and that also even from the practical considerations, granting that the activity of the plant meristems soon dilutes the antibodies beyond the point of their immunological functioning, yet in many important plant diseases the period of susceptibility is so short that the actual increase in tissues during this period could hardly be sufficient to exert any important diluting effect upon the immune bodies. It is thus unnecessary to hypothesize any mechanism of self propagation of the antibodies in plants in order to meet the argument set forth above.

A third point of comparison of plants and animals bearing on the *a priori* analysis of acquired immunity is that of the opportunities for sensitization in the two realms. The animal is subject to frequent local and blood infections which produce the effects we understand as immunological. Are plants different in this connection? On reviewing the subject of phytopathology one sees that the opportunities for sensitization are no less in plants than in animals, and perhaps greater. Beside the great number of bacterial and virus infections to which plants are subject, they also have many local and systemic fungus, algal, and vascular pathogens. They are likewise subject to toxic substances absorbed from the soil and inoculated by depredacious animals. That extracts from fungus, algal, and phaenogamous parasites may evoke specific antibody formation in animals has been demonstrated by the plant serodiagnosticians, particularly Mez and his associates. Moreover the plant is not insensitive to the presence of foreign substances, in contrast to animals. Macht (107) has found plants to be highly sensitive to certain animal poisons, much more sensitive, in fact, than are animals to the same toxins. For example, the animal toxin cantharidin although only moderately toxic to animals is lethal to *Lupinus* in a dilution of 1:50,000. Accordingly we see from our *a priori* reasoning that there is abundant opportunity for plants to be sensitized by antigenic materials, that such antigenic materials evoke antibody forma-

tion in animals, and that plants show a sensitivity to the presence of foreign bodies commensurate with that of animals. The conditions present are thus favorable to the production of an acquired immunity in plants.

A last point to consider in our comparison of plant with animal reactions is the behavior of the two types of organism in disease. The animal reaction to disease is characterized by a number of clear-cut elements of the symptom complex. We recognize among these symptoms in animal disease a production of heat, an increase in protein, and a fluctuation of the pH. Such symptoms have also been demonstrated in plant disease, the production of heat by Richards (150) and Berlese (12a), the increase in protein in plant disease by Gioelli (69), and the fluctuation of pH by Wagner (180). Accordingly, from the evidence thus far available, one is led to agree with Quanjer (143) that there appears to be no fundamental physiological difference in the symptomatic reactions of plants and animals to disease. This affords no evidence but certainly does contribute to the prediction that reactions of the zoöimmunitary type might be anticipated in plants suffering from disease.

Briefly summarizing, then, we have seen that the *a priori* arguments against the demonstration of acquired immunity in plants based upon differences in circulation, in manner of growth, in sensitivity to foreign bodies, and in reaction to disease are in no case valid objections to the thesis. We have seen, on the contrary, that there is a certain amount of evidence tending definitely toward an *a priori* belief in this capability in plants. Among the chief exponents of the *a priori* argument against this capability in plants are Blackman (22, 23) and Leach (101). Other students such as Walker (182) and Sorauer (164) have analyzed the field of plant immunity without at all considering the possibility of acquired physiological immunity in plants. On the other hand, we have a considerable number of investigators who have considered the theoretical possibility of this phenomenon in plants and who are inclined to favor this possibility. Among the latter may be mentioned Ward (183, 184), Bolley (25), Vavilov (176), and Gäumann (66) with particular reference to the immunity of grains to *Puccinia* species, Brierley (26) and East (61) regarding the recovery of plants from virus diseases, Steiner (167) concerning immunity of plants to nematode infestations, and numerous others (174, 128, 129, 159, 81, 173, 120). Carbone in his earliest studies (35) was somewhat pessimistic as to this thesis, but in later works (36, 42, 43, 44) he has taken a definitely favorable view of it. The reader interested in these theoretical considerations regarding acquired immunity in plants is recommended particularly to the works of Carbone and Arnaudi (47), East (60), Blackman (22, 23), Silberschmidt (159–161), Gäumann (66), Doussain (56), de Tomasi (174), Kořínek (81), Moritz (125, 126), and Tobler (173).

V. NORMAL ANTIBODIES IN PLANTS

In determining the presence and nature of acquired antibodies in plants it is first necessary to have an understanding of substances normally present in the unsensitized plant which exert an antibody effect upon foreign bodies. Such normal precipitating, agglutinating, or dissolving substances are here referred to as *normal antibodies*. The purposes of investigating them are twofold, first because normal antibodies occur in animal blood subject to the same laws as those governing acquired antibodies, and accordingly represent not only an important part of the mechanism of immunity but a mechanism homologous

in physico-chemical behavior with that of acquired immunity, the normal reactions thereby shedding light upon the acquired reactions; and second because in all antigen-antibody experiments control tests involving the normal reactions must be performed, and only by the understanding and elimination of these normal reactions can the acquired reactions be considered significant, i.e., truly acquired.

In order to systematize the present and subsequent discussions the subject matter will be classified primarily according to the type of reaction, whether agglutinin reaction, lytic reaction, etc., and secondarily according to the host-antigen groups. No attempt will be made to follow a rigid chronological order, since the subject content is much more clearly understood by grouping as indicated. It must be mentioned that from what we know of animal serology there is strong evidence that all of the protein reactions (agglutination, precipitation, lysis) may be due to a single type of antibody, reacting differently according to the physical form of the antigen, in which case our arrangement may be somewhat unnatural and arbitrary. However, in view of our lack of complete information on this head the present system is considered most suitable for the elucidation of the thesis. Proceeding, then, according to this scheme, we will first consider the normal agglutinins in plants, then the normal lysins, pseudolysins, antilysins, etc., next the normal precipitins, and finally other types of normal antibodies in plants.

A. Normal agglutinins in plants

As early as 1902 plant products had been tested against blood corpuscles for the determination of the presence of normal agglutinins in such products. Kobert in this year (79) tested certain plant protein solutions (ricin, abrin, crotin, and robin) against the bloods of various vertebrates including mammals, birds, amphibia, and fish, and found in many cases that these protein solutions agglutinated the blood corpuscles in very high dilution (up to 1:600,000). Extracts of bacteria also exerted an agglutinating action on such corpuscles, an indication of the wide range and probable primitiveness of the normal agglutinin reaction. The same year Kraus (95) performed similar experiments with the reactions of abrin and ricin against mammalian blood with entirely comparable results. Extracts of leguminose seeds were tested against a similar variety of bloods (mammal, bird, amphibian, fish) by Landsteiner and Raubitschek in 1907 (100). Normal agglutinins were found to be present in various cases and highly potent (reactive in dilutions of from 1:400 to 1:32,000). These were not precipitated by acid, were destroyed by boiling, were precipitated by alcohol and ammonium sulphate, and were dialyzed with difficulty. Hence they were probably protein in nature. The experiments with ricin were again repeated and confirmed by von Eisler and von Portheim in 1909 (63). This type of work was continued by Schneider in 1912 (156), who also found a very active haemagglutinating agent in bean proteose and other bean proteins. This active principle gradually disappeared from the cotyledons simultaneously with the stored food as the seedlings developed and it was not present in other parts of the plant. In the same year rice extract (Kanahara, 78) and in 1913 corn extract (Liu and Bacelli, 103) were found to contain normal haemagglutinins.

Extracts of potato tubers were found to possess haemagglutinins by Vigliano in 1922 (178), by Marcusson-Begun in 1926 (119), and by Carbone and Arnaudi in 1930 (47), while they also showed bacterio-agglutinins according to Wagner in 1915

and 1916 (179, 180) and Berridge in 1929 (20). The properties of these potato agglutinins were investigated by the various workers with interesting results. Marcusson-Begun (l.c.) found the haemagglutinins to be active in a dilution of from 1:20 to 1:50,000, weakened by heating to 60°C., destroyed by boiling (contradicted by Vigliano's findings in 1922), adsorbed by susceptible corpuscles, and later freed by warming. The bacterioagglutinins according to Wagner (l.c.) were destroyed by two hours heating at 45°C., were precipitated by $(NH_4)_2SO_4$ but again recovered in active form in the washed and redissolved precipitate, and disappeared with the approaching death of the tubers. Miss Berridge found the agglutinating power to be due to substances precipitable by 95 per cent alcohol and subsequently soluble in water, and also observed a very interesting relationship between pH of the potato sap and the agglutinin reaction, in that the agglutinating power of the potato precipitate for any one species of bacterium varied with the pH of the solution, the species differing among themselves in the respect that potato-pathogenic bacteria were not agglutinated at the normal pH of the sap while potato-innocuous bacteria were agglutinated at this pH, a condition perhaps of importance in the normal immunity or susceptibility of the potato against various bacterial species. She suggested that the agglutinative power may be due to traces of salts of di- and trivalent metals.

Agglutinins have also been found in extracts of certain of the fleshy fungi, in particular haemagglutinins in *Boletus* (Carbone and Arnaudi in 1930, 47) and bacterioagglutinins as well as haemagglutinins in *Armillaria mellea* (Vigliano 1922, 178). The latter were not destroyed by boiling. Carbone in 1904 (47), however, found no haemagglutinins in *Armillaria mellea*.

Passing now to the studies of normal agglutinins in the vegetative tissues of the higher plants, we have an abundance of data available. Normal haemagglutinins have been found in *Datura* by von Eisler and von Portheim (63) in 1909, although very extensive tests in ninety-eight other species of fifty-five genera failed to reveal such principles. A few years later Kritschewski (97, 98), found bacterioagglutinins in *Cotyledon Scheideckeri* potent at a dilution of 1:150 to 1:500, somewhat variable but present in the different parts of the plant, and apparently an inclusion of the cell sap. These were highly thermostable (to 134°–144°C.), were not subject to proteolytic digestion by pepsin and trypsin, were lost on standing 3–4 days at 37°C. and partly lost by standing at 5°–7°, and were dialyzable only in part. The active sap gave no protein reactions, the active principles were not adsorbed or inactivated by animal serum, they were capable of being so strongly bound to the antigen that neither 75°C. nor acids were able to dissociate the bond, and they were wholly held back by a Chamberland filter. He believed that the normal antibodies for the various bacteria were identical.

Beside his experiments with potato tubers mentioned above, Wagner in 1915 and 1916 (179, 180) also tested *Sempervivum* and *Beta* finding bacterioagglutinins also present in these plants, possessing the same properties as enumerated above (presumably protein). In 1922 (178) Vigliano tested a number of other plants and found bacterioagglutinins in citrus fruits, onion tubers, *Stachys* roots, carrots, cabbage, spinach, celery, salsify, and *Opuntia*, and haemoagglutinins in citrus fruits, endive, spinach, chicory, cabbage, egg-plant, cauliflower, and onions. The degree of bacterioagglutination differed in the same plant for the different species of bacteria.

The agglutinating principle in endive was filterable through asbestos.

Kořínek reports experiments in 1924 (81) with *Beta* (root extract) and *Euphorbia* (latex) in which were observed normal "agglutinins" for *Bacterium tumefaciens* in only the former species. These "agglutinins," however, were believed by the author to be entirely different from serological agglutinins, presumably acting through a simple chemotactic mechanism. The same year Carbone (37) furthered the conception of false agglutinins or to use Carbone's term "pseudoagglutinins." Such pseudoagglutinins he found in *Prunus laurocerasus* leaf extracts, the principles being particularly active against typhus bacteria, rather thermostable although destroyed by boiling, passing easily through filter paper but poorly through filter candles and not at all through asbestos, and being independent of the pH or age of the leaves. Carbone and Arnaudi then furthered their researches in this direction using *Morus* and *Salix* (45, 46). They found in the rising sap of the mulberry a haemoagglutinating and bacterioagglutinating substance and in the willow a bacterioagglutinin. These substances, however, were not always positive to all the antigenic species and varied somewhat from plant to plant. They were again relegated to the category of pseudoantibodies. Riker failed to find any normal agglutinins toward *Bacterium tumefaciens* in his researches in 1926 (152).

B. Normal lysins in plants

Passing next to the subject of normal lysins in plants, reserving analysis and discussion of all these normal reactions until a complete statement of the evidence available is before us, we find that experiments regarding lysins in plants are as abundant as those concerning agglutinins. In fact, since both agglutinin and lysin reactions are observable with the same technique and preparations, observations of the two reaction types have customarily been made by the same worker at the same time.

Kobert again paved the way in 1902 (79) for a study of normal plant lysins in showing that crotin dissolved corpuscles of rabbit and crow. In 1909 von Eisler and von Portheim in their many tests of plant extracts against blood of various vertebrates (63) found haemolysis to occur only with *Salpiglossis* extract. The following year Wilenko (188) using the complement-fixation technique, a refinement of the simpler procedure in the study of lytic reactions, observed that ricin, abrin, bean-protein, crotin, corn protein, and oat protein generally reacted against a variety of mammalian, bird, and fish bloods. The reactive substances were relatively thermostable. Wagner, whose studies with agglutination have already been mentioned, also reported in 1915 and 1916 (179, 180) positive bacteriolysis tests with potato, *Sempervivum*, and *Beta*. Here the antibody behaved just as the agglutinins in being thermolabile and precipitable but recoverable by $(NH_4)_2SO_4$. Likewise Vigliano in 1922 (178) found normal hemolysins in *Armillaria mellea* which were coctostable. In 1924 and 1925 Carbone and Arnaudi (5, 45, 46) suggested that the hemolysins found by them in mulberry were not true antibodies ("pseudo-deutero-hemolysins"). They were found in the rising sap, appeared thermostable *in vivo* but were certainly thermolabile *in vitro*, and acted particularly against sheep corpuscles but only in the presence of *fresh* rabbit serum. Arnaudi believed them to be a product of the living cells of the wood vessels. Although perhaps not strictly a lytic reaction one may recall at this point that Miss Berridge's work with potato extracts included plasmolytic reactions subject to the same comments as her agglutination reactions and probably due, she believed, to the

presence of phosphates in the potato extract. Carbone in 1904 (reported in 1930, 47) had noted an inconstant hemolytic power in *Armillaria mellea* and a hemolytic action in *Boletus* species. No normal lysins against *Bacterium tumefaciens* were found by Riker in 1926 (152).

In a series of publications commencing in 1928 Kostoff has described normal proteolysis in solanaceous extracts, demonstrated by ring testing (82, 84) and by the ninhydrin-dialysis reaction (88, 90, 91). Similar lytic rings were observed by the writer in 1931 (50) between certain oleaceous extracts, but at that time little significance was attached to them. Subsequent investigation (53) has shown the "lytic rings" to be entirely aspecific and independent of protein, occurring between extracts and certain salt solutions. Kostoff's ninhydrin-dialysis tests, on the other hand, have not yet been confirmed by other workers.

Beside lysins, antilysins, substances which inhibit the activity of lysins, have been found in normal plants. Vigliano in 1922 (178) found anti-hemolytic substances in citrus fruits, endive leaves, *Opuntia* cladodes, *Stachys* roots, and potato tubers. The active principle in the potato he found to be coctostable but inhibited by low temperatures (13°–15°C.), while it was not filterable through asbestos. The mulberry extract investigated by Carbone and Arnaudi (45, 46, 5) which was normally haemoagglutinative became anti-haemoagglutinative in the presence of certain fresh or inactivated sera. Anti-haemolysins were also found by these workers in *Prunus laurocerasus*. Arnaudi (47) also confirmed Vigliano in finding anti-haemolysins in potato tuber extract.

C. Normal precipitins in plants

Passing next to the normal precipitins of plants we again find a wealth of experimental data available, but unfortunately much of it undoubtedly involves reactions of the "pseudo" type. The first record of the presence of precipitins in plant products was that of Kraus in 1902 (95) in which he reported a sero-precipitating action of ricin solutions on rabbit blood (not on goat blood) but absence of this action in abrin solutions. In 1907 Landsteiner and Raubitschek (100) found that bean extract precipitates hen and horse sera. Three years later Wilenko (188) using ricin, abrin, bean protein, crotin, corn protein, and oat protein observed that these generally precipitated a variety of vertebrate blood sera. The precipitating power of the *plant albumens* was lost on heating them to 80°C., although the reactivity of the *sera* was not destroyed on heating to high temperatures. Moreover an excess of serum caused a decrease of precipitin reactivity. Schneider in 1912 (156), Kanahara in 1912 (78), and Liu and Bacelli in 1913 (103) demonstrated precipitins in bean, rice, and corn extracts respectively. Precipitins of extracts of bacteria and of horse and frog serum were found by Kritschewski in extracts of *Cotyledon* and of seed albumen in 1914 and 1915 (97, 98). These were active in dilutions of 1:150 to 1:200, were present apparently in the cell sap of various parts of the plant, were highly thermostable (even to 144°C.), were insensitive to proteolytic digestion, were imperfectly dialyzable, and were held back by the Chamberland filter "F." The precipitins present in *Cotyledon* were apparently identical with the agglutinins present. The plant extract used contained no demonstrable protein and it produced precipitation of human urine which also contains no chemically demonstrable protein. Precipitin and antigen in this case showed a high affinity which was not dissociated either by 75°C. or by the presence of acids. Vigliano's studies in 1922 (178) also included the finding of normal serum precipitins in citrus fruits (due to

acidity), *Opuntia*, celery leaves, and onion bulbs.

Kostoff's interest in 1928 and subsequently (82, 84, 85, 86, etc.) was primarily concerned with the precipitin reactions in solanaceous extracts. These were tested both by direct readings of the ring test and by nephelometer readings. He found normal precipitins, so-called, in many of his combinations of extracts. These "normal precipitins" were subsequently investigated by Silberschmidt who carefully analyzed the reaction techniques from the standpoint of protein reactions (161). However, Chester and Whitaker (52, 53) in an extended study of the nature of these "antibodies" found that a large percentage of the reactions called "precipitin reactions" by Kostoff and Silberschmidt were in reality simple precipitations of calcium oxalate. Four types of reaction were obtained by these workers in the thousands of tests performed. Of these four reactions the main one was the calcium oxalate reaction just mentioned. A second precipitation type (AB) was distinguished in which the reactive principles were likewise plainly non-protein and non-lipoid but organic and of relatively high molecular weight. A third reaction (MN) was the result of the interaction of two organic substances one of relatively simple structure and presumably non-protein, the other probably protein. The fourth reaction identified (XY) was so weak and infrequent as to render analyses impractical at the time of experimentation. Kostoff's, Silberschmidt's and Chester's earlier "precipitin reactions" were all found to be interpretable according to the analysis of Chester and Whitaker, which analysis now affords a suitable basis for further investigation. That most of the "precipitin reactions" reported by these workers are non-immunological, due to "pseudoantibodies" in the broad sense of the term, has been rendered evident. That some, notably the MN reaction, may possibly be of the type of serological reactions is not denied, however, even though only one component appears to be protein in nature. East has also performed a few precipitin tests of normal extracts of various species of plants including sugar cane (61). In some cases he obtained positive results. That these positive reactions are susceptible to the same sort of explanation as those of Kostoff, Silberschmidt, and Chester is presumable, although the tests of the particular species employed by East were not included in the analysis of Chester and Whitaker.

D. Other types of normal antibody reactions in plants

Our concepts and terminology of immunological reactions in plants have been largely borrowed from the serological literature. In serology the antigen is either a discrete microscopic particle (bacterium, corpuscle) or a solution usually or always of protein. The antibodies are contained in a solution (serum, tissue extract). The possible reactions are clearly distinguished as agglutination, lysis, precipitation, etc. *in vitro*, and anaphylaxis, amelioration of symptoms, or recovery, etc. *in vivo*. Plants, however, could not inconceivably display additional types of reaction. For example, the attacks of fungi on plants depend upon spore germination and penetration, mycelium- and haustorium-formation, and sporulation. Apart from the dermatomycoses, a relatively insignificant group of human diseases, there is little or no counterpart in animals to the fungus diseases of plants. This being so we must look for possible immune reactions in plants distinct from those of serology and appropriate to the peculiarities of plant sensitization and disease. A very few illustrations of such reactions in nor-

mal plants have been reported, although, as will be seen later, there is a somewhat greater number of such acquired reactions which have been observed.

In his studies in potato, *Sempervivum*, and *Beta*, Wagner in 1915 and 1916 (179, 180) described normal immune bodies which check the motility of the cilia of certain bacteria. These are analogous and perhaps homologous with the normal agglutinins described by other workers but find their expression in a reaction entirely distinct from ordinary bacterioagglutination. Moreover he also found present in these plants substances which prevent the germination of bacterial spores and of bacteria protected by thick membranes.

Carrying this type of reasoning over to the field of fungi we find a great many experiments which have been reported regarding substances in plants which inhibit growth of fungus mycelium and their relationship to immunity and susceptibility of the plants in question to the respective fungi. No attempt will be made in the present instance to review this work in detail but a few instances will be given to illustrate this point. Ezekiel, Taubenhaus, and Fudge in 1932 (63a) found that the growth of *Phymototrichum omnivorum*, a fungus causing root rot, was markedly inhibited in the undiluted although autoclaved juices from all of the resistant plants used, while profuse and heavy growth was obtained in juices from three of the four susceptible plants employed. Similarly extracts of red and yellow onions contain substances inimical to the onion smudge fungus, growth of *Fusarium lini* is partially inhibited by extracts from resistant species of flax, and some citrus bark extracts have a detrimental effect upon certain bark disease fungi. Comparable results have been obtained with corn extracts and *Ustilago zeae* and with wheat extracts and *Puccinia graminis*. For a review of the results in this field and for references to the recent literature dealing with it the reader is referred to the work of Ezekiel, Taubenhaus, and Fudge (l.c.).

In all these cases, however, there is grave question whether the inhibitory effects are due to antibodies in the zoöimmunitary sense or to relatively simple, non-immunological chemical substances present in the extracts. The presence of toxins, of unfavorable pH relationships, the lack of suitable nutrients, all these and many other non-immunological factors undoubtedly come into play in such growth inhibitions, and thus far little of the work in this field has contained definite conclusions as to the precise nature of the inhibitory substances. We must hence view such work very cautiously, reserving definite immunological conclusions till more thorough analysis is available.

E. Analysis of the foregoing data

With the data regarding normal immunological reactions of plants before us we are now in a position to evaluate these data from the immunological standpoint. Many positive results have been obtained regarding normal agglutinins, precipitins, lysins, and growth-preventive substances. To what extent are these reactions immunological in the zoöimmunitary sense, what is their relationship to acquired immunological reactions in plants, and what is their practical rôle in phytoimmunology? These are the questions which will be considered in the present section.

Regarding the nature of these plant reactions we are first required briefly to review the nature of animal antibodies and then to compare the two. Although few points regarding the animal antibodies may be stated as absolute principles, yet they have certain outstanding characteristics which are at least their usual properties. In the first place, it is generally held, al-

though not absolutely proven, that animal antibodies are proteins. The possibility of immunological reactivity seems to depend upon the large molecular size of the protein molecule, although the specificity of the reaction may depend upon relatively small radicals of the molecule. The animal antibodies are usually relatively highly thermolabile, presumably because of the coagulation of protein at the higher temperatures. Similarly they are affected by the usual protein treatments (precipitated by alcohol and $(NH_4)_2SO_4$, retained by dialyzing membranes, their solution and reactivity correlated with the presence of electrolytes, behavior as colloids). The agglutinins and precipitins are inhibited by an excess of either antibody or antigen (zone phenomenon), are readily attacked by pepsin, less so by trypsin, are destroyed by alkalies, less so by acids, and are adsorbed by suspensions such as animal charcoal. The lytic reactions are possible only through the activity of two components, one, the immune body (amboceptor), which may be identical with the agglutinins and precipitins, the other, the complement, which is present in normal serum, is non-specific, is apparently composed of two protein components, and is highly thermostable and inactive to other physical and chemical agents. With this very brief résumé of the properties of animal antibodies we may now turn to the normal reactive substances in plants.

It is necessary to use some standard for comparison between animal and plant antibodies. Such a standard, it appears from our present knowledge, is best of the following form. Plant antibodies should give evidence of protein nature, they should if acquired show specificity directed toward the antigen employed, and they should be active in relatively high dilution. How do the plant phenomena described above conform to this standard? Unfortunately many of the students of the normal antibodies have not investigated their nature and properties, and accordingly much of the evidence now available is insufficiently complete for accurate evaluation.

As regards the agglutinins we know that certain protein solutions may show a very potent agglutinating effect, comparable in delicacy to the blood reactions (see the work of Kobert and others above). It thus seems evident that the experiments performed with ricin, crotin, abrin, etc., point definitely to a homology between the normal agglutinative property of these proteins and that of mammalian blood. The agglutinins of potato are highly potent but it appears that there are at least two agglutinative principles present in potato, one of the true antibody type (Marcusson-Begun, 119) and one relatively simpler, probably non-protein, and of the "pseudoantibody" type (Arnaudi, Berridge). The reaction of plant antibodies or pseudoantibodies to heat, a most important character in serology, is not as accurate a criterion as might be desired, because of the much greater resistance of plant proteins to heat (138a). Kritschewski's "bacterioagglutinins" in *Cotyledon* (97, 98) can hardly be considered true antibodies, since they give none of the customary reactions of proteins. This same applies to the findings of Kořínek (81) and Carbone (37). The other "agglutinins" reported have not been sufficiently investigated to warrant their recognition as either true antibodies or pseudo types. We may thus conclude that so far as data are available true normal agglutinins of the serological type are present in some plant preparations but that there are also present non-protein agglutinative principles which must be carefully distinguished from the former in all critical work.

We have only one instance of normal

lytic reactions in plants which without much question is of the serological type, that of Wagner in 1915 and 1916 (179, 180). Here the active principle is plainly in the protein fraction. All other cases thus far reported, with the possible exception of Kostoff's dialysis-Ninhydrin experiments, are either clearly of the "pseudo" type (the results of Carbone and Arnaudi in particular) or are insufficiently described for accurate conclusions. Kostoff's "lytic rings" are plainly due to non-protein components, but his dialysis experiments, if confirmed, would offer valuable evidence as to the presence of true lysins in plants. Likewise the antilysins are but poorly understood. The fact that they are not filterable through asbestos, indicating that they are either of great molecular size or are adsorbed, would seem to indicate that they are protein, and if so it is presumable that they may also be of the true immunological type.

The precipitations of Wilenko's protein solutions (188) seem to be clearly of the immunological type according to our standard both in their thermolability and in their simulation or duplication of the zone phenomenon. Those of Kritschewski (97, 98) are presumably not of the true antibody type, their potency being weak (only to 1:200) in comparison with animal precipitins, and their very great insensitivity to heat arguing against their true antibody nature. On the other hand they are either of great molecular size or are adsorbed to large particles of the tissue pulp, a situation clearly suggesting proteins, yet no chemically demonstrable protein was present in Kritschewski's preparations. It is not beyond possibility that chemically demonstrable protein and immunologically active protein are distinct. Our chemical tests for protein in practically all cases are tests not for the protein nucleus of the molecule but for certain relatively insignificant radicals of such molecules, and accordingly one must not feel that absence of chemically demonstrable protein is a positive proof of the absence of serological protein. However in view of the fact that most proteins are chemically demonstrable, one may reasonably assume the probability that the precipitating extract containing no demonstrable protein by chemical tests is of the pseudo type, and that applies clearly to Kritschewski's "precipitins." The "normal precipitins" of Kostoff and Silberschmidt are certainly in most cases and perhaps all, according to the analysis of Chester and Whitaker, "pseudoprecipitins," non-protein and not homologous with animal precipitins. We thus have only the results of Wilenko pointing to the presence of normal precipitins of the serological type, we have numerous findings indicating the presence in plants of "pseudo-precipitins," and we have a quantity of data at present unanalyzable because the nature of the "antibodies" reported was not investigated.

The growth-inhibiting substances, the last of the groups of normal antibodies described above, have in no case been analyzed for their true nature. Only conjecture is permissible regarding their homology with animal antibodies, but it seems reasonable to assume that in many such cases if not in all these substances are in the same category as the pseudoantibodies described above.

We thus see that there is clear-cut evidence in the data at hand showing the very frequent presence in plant extracts of "pseudoantibodies," substances of non-protein and in some cases probably very simple structure, which through non-immunological processes produce the agglutination, precipitation, and lysis of foreign bodies. In addition there are a few cases in which the presence of normal agglutinins, precipitins, and lysins of the

zoöimmunitary type appears to be demonstrated to satisfaction. More of these should be investigated. Their nature and relationship to acquired phenomena should be better understood. The evidence presented shows that the investigation in this direction has yielded worth-while results and has opened a new field of study. We are warned of the occurrence and something of the nature of the "pseudo-antibodies" and the way is accordingly clear for a careful, critical investigation of the rôle of these two types of phenomena in plants. Moreover, the pseudoantibodies should not be rejected theoretically because of their heterology with animal antibodies. It may be that these have an important, although non-specific rôle in internal prophylaxis. The work with growth-inhibiting substances cited above certainly indicates such. And finally both as regards the true normal antibodies in plants and the pseudoantibodies, an understanding of their nature must ultimately lead to a thorough study of their function in plant disease, wherein lies the crux of the whole problem before us.

VI. ACQUIRED IMMUNITY FROM TREATMENT WITH ANTIGENIC SUBSTANCES

In the preceding section we have considered the normal antibodies in plants. With this section affording a background we are now able to proceed to the more vital subject of acquired immunity in plants. Acquired immunity may result from various manifestations of the same cause, namely the introduction into the plant of stimulative or antigenic material such as proteins or toxins. The nature of the antigen and the method of introduction serve to differentiate the various manifestations shown by the plant. In simplest form the stimulative substance may be merely injected or absorbed through the roots. Its composition is determinate, its toxic effects may be studied in a relatively simple condition, and thus the *principles* of acquired immunity may be investigated. In *practice*, in nature, the process of sensitization is somewhat more complex. Thus in a bacterial disease of a plant the reaction of the plant may be toward the whole organism (agglutination, lysis) or toward its enzymes or excreted substances, or toward the plant's own altered components (disintegration products), or toward any combination of these. Moreover, in parasitism we do not have the simple stimulation of a single injected substance, but we have many foreign substances toward which a plant is reactive which is for various reasons abnormal in its behavior, chiefly because of morbid or neoplastic reactions to parasitism. Symbiosis is a further aspect of parasitism and subject to similar modifications of the simple antigen-antibody relationships. We shall accordingly first consider the simpler situation, namely the sensitization by introduced substances of determinate composition, and then proceed to the more complex manifestations of acquired immunity in parasitism, symbiosis, and hybridization.

As was stated on a preceding page, the term antigen is customarily delimited to refer to foreign substances of protein nature which induce the formation of specific antibodies. However, this term in a broader sense includes certain non-protein toxins which induce in the plant a toleration or antitoxic reaction in many respects comparable to the usual antigen-antibody reactions and accordingly a discussion such as the present one would be incomplete without some reference to such antitoxic reactions in plants. This having been considered we may pass to the next simplest condition, namely the reactions of the plant to the introduction of protein in solution (unformed antigenic material) and

finally to the reactions of the plant to the injection of corpuscular antigens (formed antigenic material). The present section will accordingly treat in turn of these three aspects of the problem of acquired immunity to artificially introduced antigenic material.

A. Artificial introduction of non-proteins

There have been very few studies of the acquirement of immunity by plants toward non-protein stimulants. Of these, however, certain ones are deserving of mention. The Corn-cockle, *Agrostemma githago* elaborates a saponin which is highly toxic to both plants and animals. In 1918 Combes (54) cultivated various species of plants under aseptic conditions in Knop's solution to which had been added this saponin in concentrations of 1:10,000, 1:4000, 1:2000, 1:1000, 1:500, and 1:100. With all plants and in all dilutions the saponin acted as a noxious substance to the roots of the plants which did not produce this poison, while it had no toxic effect even in the strongest concentrations upon the roots of *Agrostemma githago*. Combes therefore concluded that the superficial cells of the roots of *A. githago* are immune to the saponin which this plant elaborates and accumulates in its seeds. Whether this immunity is hereditary or acquired in the strict sense of the word is somewhat questionable, but it deserves attention in the light of the apparent antitoxic effect displayed.

In 1925 Richet, Bachrach, and Cardot observed a very striking reaction of bacteria toward toxins in the nutrient substrate (151). Employing a bacterium which ferments lactic acid these workers grew the organism for several months in nutrient solutions containing thallium nitrate in varying concentrations. Then all the cultures were transferred to a medium containing .2 per cent of the salt. Their reactivity was then measured by observing their relative abilities to ferment lactic acid. Using the fermentation of the non-sensitized bacteria as a standard, these workers found that the cultures sensitized with .001 per cent and .01 per cent of the salt showed a decreased reactivity, which was interpreted as an anaphylactic reaction, while the cultures treated with .1 per cent of the salt showed a gain in reactivity over the controls of 50 per cent, a phenomenon believed to represent increased toleration or mithridatism. It is very difficult to compare with the reactions of macroscopic animals and plants those of bacteria, the individual existence of which is so ephemeral. However, considering the cultures *in toto* these results are most interesting, for not only do they yield evidence regarding acquirement of immunity (exhibited in two fashions) in a plant, but they afford evidence of such immunity in one of the simplest of all organisms, a situation pointing to the primitiveness and fundamental nature of acquired immunity. It is to be hoped that these studies of Richet and his colleagues may be further substantiated.

Carbone (37, 47) has mentioned a very brief work by Santori in 1925 (153a) in which it was claimed that plants are able to form substances neutralizing strychnine and various other toxins when the latter have been absorbed. I have been unable to find this work of Santori's and Carbone makes no further comment upon it.

Finally Leemann's work in 1932 contributes somewhat toward our knowledge in this field, although it is rather difficult to interpret his results with clearness. Leemann treated wheat seedlings in soil with various types of extracts and observed their subsequent degree of susceptibility toward *Helminthosporium sativum* (102). Certain solutions such as water extracts of *H. sativum*, bacterial decoctions and fractions

thereof, and lipase increased the resistance of the seedlings, while other solutions such as certain other bacterial decoctions, diphtheria toxin, and olive oil+lipase increased the susceptibility of the plants. This work, which suggests a non-specific antitoxic effect in some instances, is not wholly clear, not only because of the complexity and indeterminate composition of some of the introduced substances, but also because of the probable variability of the genetic constitution of the seedlings, the composition of the soil, and other possible uncontrolled factors.

We thus see that the evidence regarding antitoxic effects in plants is very limited. All, however, points in the same direction, and it thus seems probable that under some conditions at least plants can either acquire a tolerance to or actively combat foreign non-antigenic toxic material by reactions of the type of antitoxic reactions in animals. Leemann has pointed out (l.c.) the very important practical considerations arising from such a situation, and hence both from the theoretical and the practical viewpoints this subject represents a field in which a few carefully controlled experiments would be highly desirable.

B. Artificial introduction of soluble proteins

A somewhat greater amount of evidence has accumulated regarding the behavior of plants following sensitization with soluble proteins as antigens. Such behavior may take one of several forms of which anaphylaxis and precipitin reaction have been investigated in particular. Chronologically the first of these studies was that of Lumière and Couturier in 1921 (105, 106). Using *Rumex* and hyacinth leaves and onion bulbs these workers injected the tissues with varying small doses of horse and ass serum. After intervals of 30, 21, or 15 days a second dose of serum was administered with the result that the sensitized plants completely withered and died after 4–8 days, while the controls which had received only one dose (either first or second) remained healthy. The death of the sensitized plants was attributed to anaphylactic shock. Here appears to lie a clear-cut case of anaphylaxis in plants, yet these results of Lumière and Couturier have been carefully repeated in detail and with variations by Longo and Cesaris-Demel (104), Nobécourt (135), Otto and Herrig (139), Novoa-Santos and Criado (137), and Carbone (38), none of whom were able to observe any reactions attributable to anaphylaxis. Beside sera of various sorts, leucosin, a plant protein, was used for sensitization by Longo and Cesaris-Demel; beside Lumière and Couturier's plants this phenomenon was tested on *Lilium*, *Clivia*, *Impatiens*, *Lupinus*, *Begonia*, *Sambucus* and several other species of plants by Longo and Cesaris-Demel, on *Vicia* by Nobécourt, on *Lilium*, *Clybia*, *Xantedeschia*, and *Mimosa* by Novoa-Santos and Criado, on *Sedum*, *Echeveria*, *Sempervivum*, *Bryophyllum*, *Mesembryanthemum*, and *Kalanchoe* by Otto and Herrig, and on potato by Carbone. The work of these last investigators was careful and thorough, at least as much so as that of Lumière and Couturier, and some of the additional plants investigated (*Mimosa* in particular) would appear to be admirably adapted to this type of work. We are hence forced to conclude with Nobécourt that either the plants of Lumière and Couturier died from infection, or that anaphylaxis in plants is dependent upon processes yet unknown. It is of course self-evident that with such delicate reactions as anaphylaxis a single negative result is not very significant, because anaphylaxis is manifested only when the two doses are very accurately measured and spaced and when the experimental organism is sensitive to the foreign protein. However the various repetitions of this work

tend to make one rather skeptical of the results of Lumière and Couturier, particularly as one examines their figures of the "shocked" plants in which as Nobécourt points out the "plantes complètement pourrie" resemble plants killed by bacteria or *Botrytis*.

However, the view that anaphylactic shock may occur in plants, and indeed in very primitive ones, is not without some further substantiation. In 1922 Arloing and Thévenot (3) obtained positive results using as experimental organisms bacteria of several species. The serum used for sensitization was mixed with the bouillon in which the cultures were growing, a stronger dose of serum was added for the second treatment, and subsequent behavior was observed on ordinary agar. Modifications of the vegetative growth, pigment-producing power, and virulence were observed in the treated cultures, the growth in particular of the "anaphylactic" cultures being markedly inhibited.

If this work of Arloing and Thévenot is sound then not only have we another positive record of anaphylaxis in plants but we also have a further record of acquired physiological immunity in bacteria, of great interest in connection with that mentioned above of Richet and his colleagues concerning antitoxin formation and anaphylaxis in bacteria. Whatever the nature of this reaction in bacteria called anaphylaxis it has been twice recorded by two sets of observers, and it certainly suggests anaphylaxis in animals. With organisms as numerous and prolific as bacteria in a colony, it is probable that natural selection may play a far greater rôle in a short time than in the larger, multicellular experimental organisms. Such might account for the habituation of a colony of bacteria to increasing doses of a noxious substance. But in the present connection the phenomenon investigated is not toleration although it may possibly be correlated to it (power of fermentation in the first case, growth on ordinary agar in the second), and it hence appears either that there is some phenomenon in bacterial physiology simulating anaphylaxis or that anaphylaxis actually does occur in these lowly organisms and that it may impress itself upon the progeny of the "shocked" individuals. An answer to this problem is not possible at the present time, but it would be of great interest from the various standpoints of plant and animal immunity, of genetics, and of bacteriology.

Beside observations regarding anaphylaxis in sensitized plants, the only other work mentioned in the literature is that of Carbone and Arnaudi (46). These workers in their experiments with *Prunus laurocerasus* and *Morus alba* attempted among other investigations a study of the acquirement of precipitins against inoculated serum. The results, however, were not at all clear and such precipitins as were found were not specifically directed against the serum (i.e. were pseudo-precipitins).

We thus see that on the whole the work regarding the introduction of soluble protein into plants is not wholly satisfactory. The only positive results are those concerning anaphylaxis and these lose most of their significance because of the numerous failures of confirmation. Anaphylaxis or a process simulating it results from the sensitization of bacteria. In the higher plants, on the other hand, the evidence available indicates that anaphylaxis either does not occur or else it is governed by variables regarding which we as yet know very little. The precipitin technique should certainly be investigated in this connection. With the choice of suitable plants the technique is relatively simple, the precise nature of the antigen may be determined, and the results if properly controlled would be significant. The simplest

in theory and execution of the true antigen-antibody effects, it should have much to offer to the investigator in this field.

C. Artificial introduction of corpuscular or particulate antigens

Acquired immunity to the injection of corpuscles, bacteria, and similar corpuscular antigens may be exhibited in several ways, as through agglutination, lytic phenomena (lysis, antilysis, complement fixation), precipitation of extracts of the antigen, and if the antigen is living (*viz.* bacteria) alteration of its properties or lethal effects upon it. All of these manifestations of acquired immunity in plants have been studied by various investigators, and accordingly the present section will deal with them in turn.

First, as regards acquirement of agglutinins and lysins toward such antigens, the evidence is fairly abundant, although both positive and negative and both specific and aspecific results have been obtained. First in order of time are the results of Kritschewski (97) who in 1914 reported negative results from the injection of *Cotyledon* with bacteria. In 1921 Picado (141) found that injections of *Opuntia* cladodes with rabbit corpuscles or yeast cells induced neither agglutinins nor lysins. However, injection of this plant with corn pollen suspensions did result in the production of agglutinins and lysins. These pollenolysins were specific within the limits of the experiment, reacting strongly against corn pollen and pollen from other Gramineae (*Coix*, *Sorghum*) but not against that of plants more distantly related to corn; the agglutinins were less specific. Investigation of their properties showed that the pollenolysins were labile at 56°C. (15 min.), but there was also present a substance in fresh, non-immunized *Opuntia* juice (complement) which restored the reactivity to the heated extract. This work was repeated using lily pollen, but the results were not so satisfactory, since this is toxic to *Opuntia*. However, pollenolysins for lily pollen were at length obtained, active against the species of lily employed but not against other Liliaceae, yet also positive to *Gladiolus* (Iridaceae) and accordingly not family-specific as were the maize pollenolysins. In 1925, on the other hand, Carbone (38) repeated Picado's work with negative results. Carbone and França likewise failed in the demonstration of acquirement of agglutinins and lysins in leaf-extracts of *Drosophyllum*, a carnivorous plant which they had stimulated by feeding with sheep blood and with bacteria (48).

Carbone and Arnaudi did, however, succeed in the production of acquired bacterio- and haemo-agglutinins in *Morus* and *Prunus laurocerasus* in 1924 (45) using crude and elaborated plant *saps* (not *extracts*) as media to test for antibody content. These agglutinins were rather potent but non-specific, since for example a plant inoculated with cholera bacilli agglutinated this antigen less strongly than it did the Flexner dysentery bacilli. The agglutinins were coctolabile and relatively insensitive to pH. Accordingly these agglutinins are considered by these investigators as pseudoantibodies. At the same time a study of the acquirement of haemolysins and bacteriolysins failed to reveal the production of these antibodies in *Morus* and *Prunus*. The following year (46) these same workers reported further studies of antibody production in *Morus* and *Prunus*. When *Morus* was inoculated with suspensions of typhus and cholera bacteria and of *Bact. aterrimus*, the sap sometimes yielded acquired agglutinins but these were frequently non-specific. The results with the lytic tests were equally vague. When the crude sap was employed in place of the elaborated sap no acquired agglutinins

were demonstrated, but there did appear to be produced a sort of amboceptor which was highly thermolabile (destroyed by 1/2 hour at 56°C). In none of these cases was there any strong consistency in results nor specificity of antibodies. Accordingly these results confirm the earlier view of Carbone and Arnaudi regarding the pseudo nature of the antibodies. The same year Carbone (38) mentions having observed an antihaemolytic principle in potato which had been inoculated with sheep blood. On the other hand, Arnaudi in 1927 (6) observed in *Prunus* inoculated with typhoid bacteria the production of agglutinins which showed some degree of specificity, although the data given on this head are not very extensive.

Kořínek in 1922 (80) and Doussain in 1925 (56) were both unable to demonstrate the production of agglutinins or lysins in plants inoculated with bacteria. On the other hand, Much and Nyrén (127, 128, 129) have recently reported observations which seem to indicate that tubercle bacilli inoculated into living plants of certain species after several days become agglutinated *in vivo* and eventually dissolved. On the contrary the reaction does not take place in expressed sap. The various species of plants tested behaved differently in this connection, the bacteria in some instances killing the plants, in other cases surviving and propagating without injury to the host, and in yet other cases being killed without agglutination or lysis. The agglutinative and lytic principles here described, however, may have been normally present rather than acquired, and in addition their dependence upon the developmental condition of the plant (disappearing with death) has led Silberschmidt to suggest (161) that they may be merely of the type of the pseudoantibodies described by other workers.

Passing on to the subject of acquired antitoxins in plants we have the observation of Kořínek in 1922 (80) that saprophytic bacteria injected into certain vascular plants although not agglutinated nor dissolved become latent or inactive. That this may be due to an acquired toxin-antitoxin reaction is not improbable, but Kořínek's work offers no proof of this point.

Finally as regards the production in inoculated plants of substances which alter the morphological and physiological properties of bacteria or exert lethal action upon them, we are indebted to the works of Stickl in 1927 (168) and Much and Nyrén in 1930 and 1931 (127, 128, 129) for what little information is available. The former studied the effect of certain plants, notably *Tulipa*, upon typhus bacilli which were first inoculated into the plants and later reisolated. Using a great many cultures Stickl found that passage through the plant in many cases modified significantly the form and serological reactivity of the bacteria. This would appear to indicate that the plant has antagonized the bacteria by the production of substances modifying the structure and physiology of the latter. There is, to be sure, the alternate and equally sound hypothesis that such substances might have been normally in the plant and we thus are once again forced to accept the work only with reservations. The same comment applies to the work of Much and Nyrén, who found that typhoid bacteria injected into living plants of various species were in some cases so modified by the action of the host that their staining reactions, virulence, and serological reactivity became altered.

To summarize or separate the wheat from the tares in the present section is an exceedingly difficult task. We are confronted by several obstacles, failure in confirmation of experiments due to unknown variables, action of pseudoantibodies ren-

dering the acquired ones obscure, difficulty in determining whether certain positive reactions are normal or acquired, these and many other difficulties obscure the theme. A few facts, however, do stand out, for example that most of the reported cases of acquirement of antibodies deal with antibodies whose lack of specificity and other characters relegate them to the pseudo class, and that immunological phenomena *in vivo* may not be reproduceable according to the customary techniques *in vitro*. One very important concluson does follow from a consideration of these data, however, and that relates to the method of future investigation in this immediate direction. We cannot consider the problem as solved nor as much more than begun. We do know now of some of the difficulties in evaluating results. Accordingly the problem to be solved must be attacked according to some such procedure as the following:

a. The plants must be injected with antigens of determinate character, with controls, and in sufficient numbers to warrant statistical study.
b. Wide ranges of variation must be employed as regards techniques, quantity and type of antigen, species of host, time of extraction for antibodies, etc.
c. Observations must be made both *in vivo* and *in vitro* and these two carefully compared.
d. All obvious variables, genetic and environmental, must be rigidly controlled.
e. Normal reactions must be eliminated, preferably by the selection of species free from such reactions, or else by special techniques.
f. The specificity of the reaction must be ascertained by testing of the antibody extracts against a wide range of related and unrelated antigens.
g. The physical and chemical properties of the antibodies must be investigated with particular reference to protein reactions, molecular or colloidal size, thermolability or -stability, etc.

No one study before us has met all these various requirements, the omission of any one of which is fatal to a complete proof. It is neither theoretically nor practically difficult so to conduct an experiment that the results will be conclusive. One clear-cut experiment recognizing the variables pointed out above would be of more value than all of the evidence thus far secured, and it is therefore urgently to be desired that such experiments may be performed in the near future. It has been a revelation to the writer to analyze these experiments set forth in the preceding pages. Without such an analysis the field has appeared reasonably complete although somewhat contradictory in places. But on reviewing section after section of the subject matter it has been increasingly evident that there is hardly a single point which has been thoroughly investigated, and hardly one which would not be made transparent by a few carefully planned and executed experiments. A wealth of opportunity for research lies before us in this field. It is time to abandon the speculation and sketchy experimentation which have enshrouded the field and after a careful consideration of the outstanding sources of error to proceed systematically and thoroughly in the direction indicated by our perspective of the investigations thus far accomplished.

(To be continued)

PERIPATUS IN JAMAICA

By E. A. ANDREWS

"Peripatus is one of those animals whose presence lends a distinct character to the fauna of any region." WILLEY.

THE finding of Peripatus in a part of Jamaica B. W. I. not previously known as its habitat (incidental to a molluscan study aided by a grant from The National Research Council) may justify some consideration of the previously known distribution of this remarkable animal in that island.

The enigmatical nature of Peripatus was not fully appreciated till increased knowledge showed it presented in one animal traits previously known only in different groups; so that it was a puzzle such as might be some imagined simple animal showing the outside appearances of a dog along with, let us say, the internal gills of a fish. But finally it has become customary to place Peripatus in a distinct group of some fifty species approaching insects and centipedes, in a simple way, but with some features of annelid worms. They are found not only in the West Indies but in Central and South America, in Central and South Africa, in Australia and in Indo-Malaysia.

THE HISTORY OF PERIPATUS

Its worm-like appearance led to its being called an annelid and the two first known specimens in the British Museum were designated in manuscript *Nereis pedata* and *Nereis viridis* by two different zoologists, in the period when "Nereis" was rather a common name for many annelid worms. One of those two specimens was in the collection of Sir Hans Sloane, who was in Jamaica in 1687, but Bouvier concluded this specimen came from Dominica in the second half of the eighteenth century, toward 1760 probably, which, however, was seven years after the death of Sloane, at the age of 93.

Subsequently the first published account of the creature emphasized its resemblance to a mollusc, a slug; but this opinion was never taken up by any one else and for long the animal was assigned by some to the annelid and by others to the myriapod group, till wider knowledge of its anatomy and development furnished more complete evidence of its position near assumed ancestors of the insect group. That Peripatus looked like a slug was the impression gained by the Reverend Lansdown Guilding, when, long resident in the island of St. Vincent, he had in mind to write a complete fauna of the West Indies, but sought first to send back to England essays on all the main groups of animals looked at from three points of view: as injurious to man (*Pestes occidentales*) as objects of special wonder and interest (*Miracula zoologica*) and as being of direct use (*Usus animalium*). His contribution in 1825 belongs decidedly to the second category, for he there figures and describes the paradoxical creature he first named Peripatus. He found it by chance amidst plants he had collected at the foot of a certain great mountain. As one who had described certain new slugs apparently he saw in the slow movements, the possession of two retractile feelers, the soft velvety skin, along with the habit of ejecting glue-like material when disturbed, sufficient suggestions of slug life to overweigh the fact that the animal moved by distinct legs,

which, in fact, led him to the name Peripatus as having "ambulacra" or paired rows of legs like an avenue of trees and also induced him to place this animal into a new class "Polypoda;" thus, as he recognized, playing havoc with the group Mollusca that was well known to contain no animals with pairs of legs on the sides of the body. This sole specimen had 33 pairs of legs, all alike, and as it walked along on them like the common milliped, julus, he gave it the specific name *Peripatus juliformis*.

His excellent figures in color and concise Latin descriptions established the reality of this phenomenal animal without doubt, even though the author, in recognition of his remoteness from libraries, said: "I must request that, with the exception of the drawings, everything I may send back to England on subjects of natural history may be examined with the greatest caution and suspicion." Thus in Guilding's description under the heading Mollusca Caribbæana in the *Zoological Journal* of London, this problem creature was well introduced into scientific circles.

As years went by, other species of Peripatus were discovered in various West Indian islands, in South America and even at the Cape of Good Hope till finally in Jamaica, twenty years after Guilding's discovery, the well-known naturalist of the old school, Philip Henry Gosse, after his zoological work in England and in Canada, while then resident at Bluefields in the western part of the south coast of Jamaica, and well conversant with the animals of Jamaica, found five or six creatures that he recognized as like Guilding's Peripatus, but which, he thought, to be more like annelids than like molluscs. He found them when searching amongst stones in a burnt-over region not yet grown up with vegetation and close to virgin forest at the base of a conical peak in the mountains four or five miles from Bluefields.

Three of these lasted on in the British Museum to be studied in succession by three authorities. Nothing more was known of Peripatus in Jamaica for nearly fifty years, but then in 1892 a local naturalist versed in the study of insects, Mrs. E. M. Swainson, found some seven Peripatus on Beacon Hill about a mile from Bath, in the eastern part of the island and thus more than a hundred miles from Gosse's Bluefields. Some of these specimens were sent to the headquarters of science and art in Jamaica, The Institute of Jamaica, where they were studied by Dr. M. Grabham and by T. D. A. Cockerell, who noted such differences from the account of Guilding that they decided to recognize a new species *Peripatus Jamaicensis*.

The region of Bath has since then remained the chief source of knowledge of this animal in Jamaica; but in 1897 when the Johns Hopkins Marine Laboratory was located at Port Antonio, on the north coast, when a chance outbreak of yellow fever caused the death of both Professor Humphrey and the zoologist of promise, Dr. Conant, the latter found one specimen of Peripatus at Blue Hole, to the east of Port Antonio, thus adding a third locality situated 120 miles from Gosse's and 15 from Bath. Thus Peripatus was known at points in a large area, but yet very few specimens had ever been seen when in 1901 a request for more specimens to be sent by Ray Lankester to Professor Bouvier for use in his great monograph of the Peripatus species of the world, was met by activity at The Institute of Jamaica. J. E. Duerden found that after the original seven sent in 1892 from Bath to the Institute a dozen more reached Dr. Grabham in 1893 and after that but two or three were found in scattered localities; they seemed rare indeed since collectors could find

none. Advertisements in the papers brought no results; but when Dr. Duerden collected some and exhibited them with offers of reward, the natives soon found them in large numbers; 50 were brought in and Dr. Grabham also obtained a large supply; then eighty more came, and fifty more were offered. All these were found under stones and rotten wood and often buried in the earth. By comparative study Professor Bouvier found that some 24 of these specimens were properly to be called *Peripatus jamaicensis*, but some 72 were a variety of Guilding's *Peripatus juliformis*, to be called var. *Swainsonae*. Gosse's original specimens also proved to be of the same two; and all the specimens thus far found in Jamaica are referred to these same.

A NEW LOCALITY FOR PERIPATUS

In March and April 1909, Thomas Barbour demonstrated the abundance of Peripatus near Bath by finding some hundred specimens. A fourth locality for Peripatus in Jamaica was found in 1910 by the present writer, at the head of row-boat navigation in the Great River to the east of Montego Bay on the north coast, less than 20 miles from Gosse's place of discovery and 100 miles from Bath; thus establishing the existence of Peripatus at the four corners of a great quadrilateral one hundred miles long and fifteen to twenty wide; however, only a single specimen was obtained at each of the north coast localities. Within this major area of some 2000 square miles, nearly half of the area of the island, no localities for Peripatus were recorded till the present July 29th, when one specimen was taken in searching for small molluscs amidst dead leaves in a region along the road from Kingston to Stony Hill, so often traversed as on the way to Castleton Botanic Gardens. This new locality is twenty-five to thirty miles from the two known localities in the east and about eighty from the two in the west part of the island that form the corners of the above mentioned quadrilateral. This fifth locality is but little above Constant Springs and not five miles from Half Way Tree, in fact scarce seven miles from the Institute of Jamaica, but though so near the center of a dense population it is perhaps secure from destruction, as being along the water-works reservation.

More precisely described, this new locality may be found by leaving the road below the bend by a gate on the right at a sign marked by the Board of Public Works. A trail here leads up along the water pipe and then along the open "gutter" carrying water from the Hermitage dam presumably. About 440 paces from the gate the trail bends to the right as we note a low arch in a wall allowing water to pass across the road down to the right, on occasion: here, on the left, lie large exposures of rough limestone, on top of which the Peripatus was found amidst dead leaves shaded by the dense brush of the hillside. Removing leaves the Peripatus was accidentally seen partly projecting from under the dead leaf and taken to be perhaps a slug, but as when picked up it discharged its glue in fine threads adhering strongly to the fingers, clear and nearly tasteless, and moved with caterpillar-like legs, while in the light revealing the beauty of its velvety skin, it was recognized as Peripatus. Allowed to crawl on the hand it quickly sought the under, shaded side and in a bottle amidst dead leaves it came to rest out of the light. Search for another specimen was fruitless, but the time available was but scant.

PERIPATUS AS A TRAVELLER

Amidst these dead leaves in the bottle with much moisture and frequent airing

it lived on not only the few hours before sailing but all the trip to Baltimore and then in a larger glass dish it kept its quiet existence till September 8th.

Though this is the first living Peripatus to emigrate from the West Indies, Dr. Grabham saw living Peripatus from New Zealand and the Cape at Cambridge with Professor Sedgwick, who states that he went to the Cape in the middle of August, 1883, collected and brought back over three hundred living Peripatus, of which some lived on till the following July; while Walter Heape brought back some more living ones in 1884 and another large shipment of living Peripatus collected at Table Mountain was sent on in the winter of 1884–5. Moreover, while two successive attempts to import living Peripatus from New Zealand to Cambridge were not successful, since the animal died on the long voyage, yet a third attempt succeeded when the Peripatus were kept in a special cool part of the ship. Two of these went a further journey to Würzburg. Living Peripatus were kept in the museum in South Africa where Sedgwick saw with astonishment the 30 or more young just born and some of them crawling upon the back of the mother.

Bouvier also received one living Peripatus sent from the Cape to Paris in a small box full of wet moss. This specimen was then kept in a glass dish with the moss, earth and bits of decayed wood till it finally escaped from under the lid, after being studied for some time. Other specimens have been carried home and kept alive. In Australia, Fletcher kept one Peripatus alive for three or four months, in a tin; he also collected and brought home 100 healthy specimens, many of which were kept nearly a month, during which time they gave birth to young; but in some very hot weather they developed blister-like swellings on the head, and then were killed. Evans in the Malay Peninsula chopped into dead stumps and found Peripatus dormant within dry wood 4–5 feet above ground and also found them in fallen logs. But in South America he reports a native found Peripatus amidst dead and decayed tree trunks and leaves and nine specimens brought to Georgetown, British Guiana, were kept alive in a glass jar kept very wet, as in an artificial swamp. Another American species was also kept alive in these very wet conditions. Previously in that region Slater had found Peripatus exceedingly scarce under rotten logs and decayed palm stalks, but had taken 20 of them from Demarara to England alive, but suffering from cold.

In Trinidad, Kennel observed that though usually but one Peripatus was to be found isolated here and there yet in a very dry season 60 were found under one small decayed branch where they had sheltered to avoid the dryness of day. He also kept dozens of Peripatus in tins with rotten wood for weeks without food, but when too dry many died, yet others revived in wet air, though they avoided liquid water. Later some of these revived specimens took the long journey to Europe though here again some died after four weeks when sufficient moisture was accidentally omitted; others arrived alive and one of them went on to Würzburg to be kept alive in Semper's greenhouse.

In Jamaica, however, Peripatus has not been a good traveller, for while Grabham and Cockerell say of the three specimens sent by Mrs. Swainson to Kingston that one was still alive, this was a great exception; in fact Barbour makes use of the delicacy of Peripatus to strengthen his arguments that Jamaica had not been stocked by chance transport of animals over the sea but by migrations over land connections formerly existing. He says:

Peripatus is one of the most delicate of known organisms. Dr. Grabham, a well known field naturalist, long resident in Kingston, Jamaica, tells me that with the greatest care he had never been able to bring living Peripatus from Bath to Kingston, a distance of 35–40 miles and my experience has been exactly the same. Last winter it was found absolutely impossible to keep alive at all any of the hundred-odd specimens which were taken in the vicinity of Bath. On the return from a day's collecting many dead specimens were always found in the receptacle in which they were carried, which was filled with the natural earth and moss taken from the spot where the creatures were found.

Conceivably these Jamaica Peripatus might have travelled better had they the extreme moisture and avoidance of heat that is reported as necessary for some other kinds of Peripatus on long journeys; moreover, the presence of coiled dead leaves within which the Peripatus may lie concealed may be of aid in transportation as well as in normal life on the forest floor.

While the present solitary specimen shows that long journeys may be made on shipboard without death, whether a Peripatus concealed within a tree trunk could be carried, floating, across salt water can scarcely be decided till experiments have been made to test the resistance of Peripatus to salt water. Excepting for contact with salt water the air, water, moisture, temperature, conditions within a tree trunk and within a bottle on shipboard seem not so very different; and enveloped in a film of air could the animal escape contact with salt water? Gosse said of the specimen he found "The skin repelled both water and spirit when immersed." Likewise Willey found that Peripatus collected in the island of New Britain floated on water and when immersed was covered with a beautiful sheen of air. Similarly this last specimen from Jamaica, though living amidst very wet leaves, always remained dry, supported on its legs above the water and protected by the peculiar skin surface and when dead it floated on Carl's solution and when shoved under was coated dorsally by a thin film of air, as in some diving insects, stretched over its rows of papillae, and collected in larger areas just above the bases of the legs; but the shrivelled antennae held no air.

As a witness against the old "flotsam and jetsam" theory of the peopling of such islands as Jamaica, Peripatus stands in need of further cross questioning. Could it be shown that migrant birds transport living snails, one might invoke Peripatus glue and coiled dead leaf as aids to such aerial transport. Once transported a single pregnant female might populate a new region.

DESCRIPTION AND BEHAVIOR

The present successful Jamaican specimen is of full size for the species, stretching out alive to 75 mm. and dead 74 mm. with width and depth of about 5 mm. while the antennae were elongated by the animal to 7 mm. but in death shrivelled to scarce 3 mm. Alive, the plump well-fed appearance of the animal is enhanced by the rich velvet of skin which excels in the Jamaica Peripatus, for Sedgwick, after expressing great admiration for the beauty of Peripatus, said of the Cape species: "These animals so far as skin is concerned are not surpassed in the animal kingdom." And yet Dr. Grabham who saw those same Cape specimens remarked of the Jamaica species; "In point of beauty the skin certainly surpasses both the New Zealand and the Cape species."

The color of the present specimen was greenish mixed with brown; the transverse rows of tubercles on the back being yellow with dark-red-black central spines and with pale green transverse grooves in advance of the tubercles; the underside was pale flesh color. The antennae did not have the white tips common in *P.*

jamaicensis and the skin sculpturing together with the 34 pairs of legs led one to identify it as a female specimen of *P. juliformis* var. *swainsonae*. When placed after death into Carl's solution, which contains acetic acid, the green color rapidly disappeared, leaving a dull maroon, much lighter below and this persists in alcohol.

Like all known Peripatus, this one in Baltimore showed the strongest negative reaction to light, walking rapidly away whenever light fell on its head, or going backward to escape it; being active only at night and remaining all day concealed under dead leaves or buried in rubbish. Its marked habit was to select some coiled-up leaf and to rest within its protection lying on the dead leaf and covered by its coiled-over part. Thus concealed it was difficult to find in a dish of leaves, especially as it remained quiet when the leaves were moved about. No doubt such hiding within coiled dead leaves would make discovery of specimens on the forest floor very difficult.

At rest, this Peripatus was not seen to coil up with ventral side inward, as seen by Bouvier in a certain species, but was coiled back and forth in various shapes with ventral side down, as a rule, though the body might be twisted so that some of the legs were uppermost. Moving about outside its resting place it showed a tendency to walk along the edges of solid objects and the same preference for contacts seemed shown in the habit of moving along on its own body; that is, it adopted many attitudes of hooks and parallel lines as it turned its head backward and crawled along itself. It was not seen closely coiled but a cross section might have shown its body cut three times. Within its preferred leaf lodge it would readily turn end to end like a myriapod or many other animals used to dwelling within cavities.

Placed out in the light it walked with raised head swaying from side to side, testing everything with its antennae, as described by Bouvier. Each leg swung back a wide arc, broke suddenly from its attachment and passed swiftly forward close to the preceding foot, which is raised as the advancing foot is clapped down in its most forward position to anchor to the substrate.

Quite like some insects, the Peripatus was seen to clean its antennae with its mouth, but it elongated them and bent them down like an elephant's trunk to draw them through the mouth which was everted to show the jaws. First one, then the other antenna was thus treated.

THE FOOD OF PERIPATUS

Knowledge of the natural food of Peripatus remains unfortunately very meager. The chief record of direct observation is that of Capt. Hutton in 1876 who found Peripatus in New Zealand in decayed wood, under stones or in crevices of rocks and kept them under observation, stating that they do not feed in winter though still breeding and that they feed in the night but also in the day time when hungry. He says "I have seen one shoot out its viscid fluid from the oral papillae at a fly introduced into the jar in which it was confined and stick it down; it then went up and sucked its juices, rejecting the whole of the integument."

Sedgwick in 1888 said that of the food in nature we know nothing but that in Cambridge Peripatus ate the entrails of their fellows and also their embryos and also liked raw sheep liver. Bouvier found in dissecting many specimens of several species chitinous fragments of insects, but also pieces of vegetable tissue he thought might have been in the food of the creatures eaten by Peripatus. He failed to induce the captive Peripatus to eat earth-

worms or wood-lice. Kennel was not certain, but thought that Peripatus ate little termites and also snails and little worms; but he never saw them eat. In captivity his Peripatus ate drops of its own glue and Kennel inferred that in nature it may eat its prey and glue at the same time.

Nothing is directly known of the food of the Peripatus in Jamaica. Cockerell speaks of their casting out glue in a network that holds the insects used as food, but, as Bouvier remarks, it is not clear that this was direct observation upon Jamaica specimens, but it seems rather part of Cockerell's account of the habits of Peripatus in general.

In Baltimore attempts to feed with pieces of earthworm and crushed insects were apparently without success; on the other hand there was as considerable evidence that the animal bit out pieces of dead leaf; and fragments of dead leaf, as well as very small amounts of insect remains, were found in the faeces. Possibly the reported long continuance of Peripatus in good health without apparent food, but with presence of decayed wood and the like, may be in part due to some ability to use dead vegetable matter as food.

A few days before its death this Peripatus was transferred to a large formicary, 7 mm. deep, in which it walked some 42 cm. through a zig-zag passage from the light to take up its abode in a coiled leaf, see Figure 1. From this place farthest from the window-light, screened by opaque paper it apparently walked back at night to the point of ingress and ate from a slice of apple a depression 4 by 4 by 2 mm. A small bit of the apple, 2 by 1 mm. was found close to the head end of the animal, outside the leaf, the next day, when the Peripatus was back in its leaf, but dead. Examined that night by red light without other disturbance the Peripatus discharged its glue from the head end and then from the hind end of its retreat as if irritated by the light, but the next day three small red ants were found dead, within the leaf close to the Peripatus as if they might have been involved in the irritation.

The discharge of glue when irritated is one of the remarkable responses of Peripatus. Evans in the Malay Peninsula saw a captured Peripatus cast its glue 18 inches. Kennel says in other species the glue is thrown two to three feet and

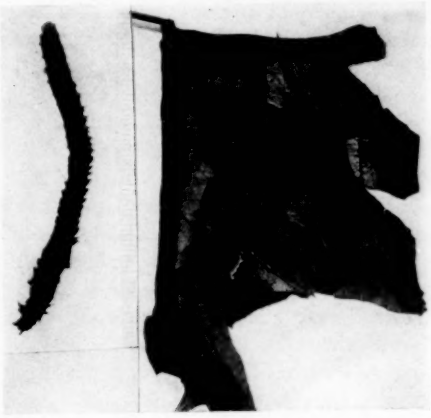

FIG. 1. DEAD PERIPATUS WITHIN CURLED OAK LEAF ON RIGHT, HEAD CONCEALED, TAIL ABOVE; REMOVED ON LEFT OF MILLIMETER SCALE

striking an obstacle spatters to form a network of fibers, but, though sticking on one's hands so that it cannot be removed without soap and water, it does not adhere to Peripatus itself. This present specimen discharged its glue several times when picked up at long intervals; once making on the finger under a bit of dead leaf a puddle 5 by 5 by 2 mm. that held the 14 grams weight of metal forceps. The long glue threads stretched between one's fingers spring back like rubber and are beaded with small drops each of which when touched

with a needle can be drawn out as a long side thread. Apparently this should be very effective for entangling small insects.

THE DISTRIBUTION OF PERIPATUS

Returning to the known distribution of Peripatus in Jamaica we gather from the maps of R. T. Hill that the five localities where it has been found are about the 1000 foot level, or below it; while in Australia, Peripatus has been found all the way up to 5700 feet where it was collected by Fletcher in regions where for 4–5 months snow lies several feet deep. Moreover, in two of the above five localities in Jamaica it was closely associated with rough limestones and probably so likewise in the original locality near Bluefields, as well as in the locality at Blue Hole, but in the fifth where most have been found the rocks are much more complex; though there may be some hard limestones there. This Bath region is on the older Eocene and Cretaceous formations but all the other localities on the prevailing Oligocene limestones of deep sea origin, though the Blue Hole occurrence may have been on recent raised coral rock.

Possibly Peripatus may live in some of the regions of Jamaica where not yet known, but that Peripatus may occur in all or much of the region intermediate between the five known points is by no means certain. In two localities apparently alike, Willey found Peripatus in only one and remarks: "the extremely local, or sporadic, occurrence of Peripatus is well known."

SUMMARY

The finding of Peripatus in a fifth locality in Jamaica shows that it ranges sporadically over near half the island at elevations under, or near, 1000 feet, often on limestone formations, in damp woods, on or in dead wood and earth and dead leaves especially.

Previous inferences that the Jamaica Peripatus species were excessively delicate and impossible to transport alive need to be modified, since this last discovered specimen was brought to Baltimore and kept a month in captivity. In the past other species in New Zealand, South Africa, Trinidad, South America and Australia have been carried long distances and kept in captivity.

Inferences that Peripatus could not possibly be disseminated from land to land across seas are not entirely binding, but await experiments as to the ability of Peripatus to remain alive if exposed to salt water.

While the food of Peripatus remains still too largely unknown, this Jamaica specimen offered some hints that dead vegetation may form a part.

LIST OF LITERATURE

1826—Guilding, L. Mollusca caribbæana. Zoological Journal, vol. ii, p. 437–444, Pl. XIV. London.

1851—Gosse, P. H. A Naturalist's Sojourn in Jamaica.

1876—Hutton, F. W. On Peripatus novae-zealandiae. Ann. Mag. Nat. Hist., (4) XVIII, pp. 360–369, Pl. XVII.

1883—Kennel, J. Biologische und faunistische Notizen aus Trinidad. Arb. Zool. Inst. Würzburg, 6, pp. 259–286.

1885—Sedgwick, A. The development of Peripatus capensis. Quart. Jour. Micro. Sci., 25, pp. 449–468, Pl. XXXI–XXXII.

1887—Slater, W. L. Notes on the Peripatus of British Guiana. Proc. Zool. Soc. London, pp. 130–137.

1887—Fletcher, J. J. Proc. Linn. Soc. N. S. Wales, (2), vol. VII, pp. 179–196.

1888—Sedgwick, A. A monograph on the species and distribution of Peripatus (Guilding). Quart. Jour. Micro. Sci., 28, pp. 431–493, Pls. XXIV–XL.

1892—Grabham, M., and T. D. A. Cockerell. Peripatus rediscovered in Jamaica. Nature, XLVI, p. 514.

1893—Cockerell, T. D. A. Notes on Peripatus jamaicensis Grab. and Cock. Zool. Anz., XVI, pp. 341–343.

1893—Grabham, M. Peripatus Guilding. Journal Institute Jamaica, vol. 1, pp. 217–220.

1899—Hill, R. T. The Geology and Physical Geography of Jamaica. Bull. Mus. Comp. Zool. Harv., vol. XXXIV, pp. 256, Pl. 1–41.

1901—Evans, R. On two new species of Onychopora from the Siamese Malay States. Quart. Jour. Micro. Sci., XLIV, pp. 473–538.

1901—Duerden, J. E. Abundance of Peripatus in Jamaica. Nature, LXIII, pp. 440–441.

1901—Cockerell, T. D. A. The Jamaica species of Peripatus. Nature, LXIII, pp. 325–326.

1902—Willey, A. Zoological Results, etc. Part I. *Peripatus novae-britanniae*. pp. 1–51, Pls. I–IV, Cambridge.

1903—Evans, R. On Peripatus Guianensis (sp. nov.) Quart. Jour. Micro. Sci. 47, pp. 145–160, Pls. XIII–XIV.

1905—Bouvier, M. E. L. Monographie des Onchophores. Ann. Sci. Nat. Zool., T. II, pp. 1–383, Pls. I–XIII.

1907. ——. *Idem*. T. V., pp. 61–318.

1910—Barbour, T. Notes on herpetology of Jamaica. Bull. Mus. Comp. Zool. Harv., vol. LII.

1911—Andrews, E. A. The Jamaica Peripatus. Notes from the Johns Hopkins University Laboratory at Montego Bay, Jamaica, Summer 1910, J. H. U. Circ. Feb. 1911.

THE FLORA OF THE HAWAIIAN ISLANDS

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THE study of the vegetation of any region, its composition and relation to its environment may be of great interest to the botanist; but far more important is a study of the origin of the plants composing the flora and their relationships with those of other parts of the world. Such studies may furnish important data, both to biologists and geologists, as they often throw light upon changes in land connections and the corresponding distribution of the waters of the oceans, such changes involving marked climatic effects as well.

In some extensive areas in the north temperate zone, the history of the vegetation is revealed both by a study of the living plants, and the fossils. It is evident that the northern parts of both Eurasia and North America have been more or less intimately connected from a very remote period.

Throughout this whole region, from Western Europe to Canada and New England, the predominant trees are much the same—pines and firs, poplars, willows, birches, maples, oaks, etc.—and the shrubs and herbs show a similar relationship. While there are many differences in detail, the essential character of the floras is the same. Where there are marked differences a study of the fossil plants shows that some of these are due to the extinction of once widespread types which are now greatly restricted in their range. The Californian Sequoias, the bald cypress of the Gulf States, and the tulip tree (Liriodendron), are examples of such once cosmopolitan trees.

The conditions in the south temperate zone are very different, and the widely separated continental areas—Africa, South America and Australia,—differ much more from each other than is the case in the north temperate zone. Moreover our knowledge of the fossil plants of these regions is still very incomplete.

The floras of these isolated regions show a high percentage of endemic species, and this is also the case in such large islands as Madagascar, Juan Fernandez and New Zealand. It reaches its most extreme expression in the Hawaiian Islands, the most isolated area of equal size in the whole world.

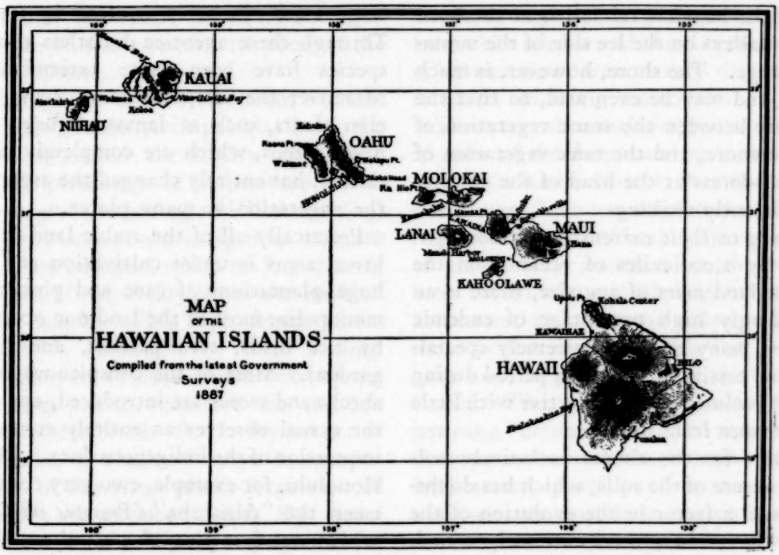
The Hawaiian Archipelago consists of a chain of islands extending from northwest to southeast, between latitude 18°55′ and 21°15′. Its total area is 6,454 square miles, of which the southernmost island, Hawaii, comprises about two-thirds. To the northwest, there is a series of small islets and reefs, extending for about 18 degrees. All of the islands, except for the coral reefs, are volcanic; but at present volcanic activity is restricted to Hawaii, whose two giant craters, Kilauea, and Mauna Loa, from time to time furnish volcanic outbursts of spectacular proportions.

In the older islands no evidences of recent activity can be found, and the disintegration of the volcanic soils is complete; in Hawaii, however, and to a lesser degree elsewhere, there are expanses of bare lava, nearly or quite destitute of vegetation.

The volcanic activity has evidently

developed along a rift beginning at the northern end of the archipelago, and has proceeded southward, and now is found only in the active craters of Hawaii.

There is abundant evidence that the larger islands were formerly united into a single much larger land-mass, which through long subsidence has gradually segregated the existing islands. That the northern island, Kauai, was first detached, is indicated both by the deep and broad channel between it and its neighbor to the south, Oahu, and also by its very highly specialized flora, the proportion of endemic species being greater than in any other island.



Upon Oahu is Honolulu, the main city of the territory. Between Oahu and Hawaii are Molokai and Maui. Two smaller islands, Niihau, off the coast of Kauai, and Lanai, near Molokai, may also be noted.

The topography, especially in the older islands, is excessively rugged. The windward districts are drenched with torrential rains, deposited by the moisture-laden Northeast trades. The resulting erosion has cut deep and precipitous canyons with almost vertical walls, "palis" in the vernacular, whose brinks, concealed by dense vegetation, are a serious menace to the incautious explorer.

The effects of erosion on the windward coast of Hawaii are very evident as the steamer approaches. The openings of deep gorges are visible, cutting through the high vertical cliffs, and often discharging a cataract which plunges into the sea. The writer visited the head of one of the largest of these canyons, Waipio Gorge, whose vertical walls are 3,000 feet deep. Over the edge of this canyon, cataracts fell, reminding one of some of those in Yosemite.

In the older islands, e.g. Kauai, Oahu, the mountains are much worn down and the highest summits are only 4,000–5,000 feet elevation. In the most recent islands,

Maui and Hawaii, the great volcanic cones are much higher, Haleakala on Maui being 10,000 feet, and Mauna Loa and Mauna Kea nearly 14,000 feet. The latter (13,675 feet) is the loftiest peak in Polynesia.

On these high islands nearly all the moisture is precipitated on the windward (N. E.) side, but in the lower islands much of the moisture is carried over the mountain summits and falls on the lee side. This is well shown back of Honolulu, where the heaviest rainfall is at the head of the valleys on the lee side of the mountain range. The shore, however, is much dryer, and may be even arid, so that the contrast between the scant vegetation of the lee shore, and the rank vegetation of the rain-forest at the head of the valleys, is sufficiently striking.

Owing to their extreme isolation, separated by 2,000 miles of ocean from the nearest land mass of any size, there is an exceedingly high percentage of endemic species, many of them extremely specialized and testifying to a long period during which evolution has been active with little disturbance from outside.

Except for the almost exclusively volcanic nature of the soils, which has doubtless been a factor in the evolution of the flora, the conditions are extremely varied. With elevations ranging from sea level to nearly 14,000 feet, there is a corresponding range of temperature from tropical heat in the lowlands, to regions almost of perpetual snow. The variation in rainfall is equally striking, ranging from an annual rainfall of 400–500 inches to less than 20 in some of the dry leeward districts. These extraordinary ranges in elevation, temperature and precipitation, occurring within so limited an area, afford the biologist an unusual opportunity for studying a wealth of problems of the greatest importance in plant evolution. Considering the latitude the temperatures are very moderate.

Unfortunately for the botanist, much of the original vegetation in the lower districts has disappeared since the advent of the white man. During the past fifty years nearly all of the available land at the lower elevations has been brought under cultivation, and the forests have disappeared. The ravages of cattle and sheep, and in the dryer parts of the islands, goats, have also completely denuded large areas, formerly covered by forest. Through these agencies doubtless certain species have been quite exterminated. Moreover the introduction of many foreign plants, such as lantana, guava and many weeds, which are completely naturalized, has entirely changed the aspect of the vegetation in many places.

Practically all of the arable land in the lower areas is under cultivation and the huge plantations of cane and pineapples monopolize most of the land not occupied by rice fields, taro patches, and home gardens. Most of the conspicuous trees, shrubs and weeds are introduced, and give the casual observer an entirely erroneous impression of the indigenous flora. About Honolulu, for example, two very common trees, the "Algaroba" (*Prosopis juliflora*), which was first planted more than a hundred years ago, and the "ironwood" (*Casuarina equisetifolia*) a later introduction, seem to be thoroughly naturalized, and might very well be supposed to be really natives. Many foreign weeds are thoroughly established, and in the hills back of the city, one encounters almost impenetrable thickets of lantana and guavas—escapes from gardens which have become veritable pests. In the dryest places prickly pear cactus, introduced from Mexico, and a thorny Acacia (*A. Farnesiana*) are abundant. In the moister places, some very attractive exotics have

become naturalized. Wild ginger (*Hedychium coronarium*), cannas, morning glories, passion flowers, are common along the roadsides and in the woods and the moist valleys back of Honolulu.

The climate permits the cultivation of most of the tropical fruits—mangoes, avocados, papaya, custard apples—and many others, and a profusion of showy flowering trees and shrubs adorns the gardens. Among the shrubs, especially in Honolulu, are many varieties of Hibiscus, some of which are hybrids of the common *H. rosa-sinensis* with some of the native species.

As might be expected from the extreme isolation of the Archipelago, both the flora and fauna are highly specialized and the percentage of endemic species is very large. According to Hillebrand (25) 75.93 per cent of the indigenous vascular plants are endemic, while no less than 85 per cent of the dicotyledons are confined to the islands. This high degree of endemism is confirmed by later studies. According to a recent enumeration of the flowering plants, furnished me through the kindness of Mr. E. H. Bryan, Jr., of Honolulu, a total of 1,052 indigenous species of flowering plants is given. Of these 163 are monocotyledons, 889, dicotyledons. Of the former 119 species are endemic, of the dicotyledons 832. This extraordinary degree of endemism is probably unequalled in any other region of the world. A somewhat similar condition obtains in New Zealand, but perhaps owing to the much cooler climate, the number of species, especially of dicotyledons, is relatively less than in Hawaii. The latter, although only about 1/16 the area of New Zealand, has approximately two-thirds as many species. According to Cockayne (16), the total number of vascular plants in New Zealand is approximately 1,780, and the percentage of endemism nearly as great as in Hawaii, viz., 74 per cent for all the vascular plants, and 85 per cent for the dicotyledons.

There are two very different theories as to the origin of the archipelago. Hillebrand (25) and others believed that the islands were elevated above the sea through volcanic action starting in the ocean depths, and that they have always been completely isolated. At present the water of the surrounding ocean is very deep. Within forty miles, depths of upwards of 10,000 feet are found, and between the islands and the American coast is an enormous area of very deep water, in places exceeding 20,000 feet.

There are other students, however, who, in spite of the deep water now surrounding the islands, believe that they have not always been so completely separated from other bodies of land. The advocates of this theory assume that the islands were united into a much larger area than at present, and that this was connected, more or less directly, with the Australasian and Malayan regions in the Southern Pacific. The multitude of islands constituting Polynesia is believed to be merely the remnants of once much more extensive land-masses, possibly of continental dimensions, so that these scattered islands are the remains of mountain masses that have been in subsidence possibly since early Tertiary times.

While between Hawaii and North America there is an enormous and continuous area of very deep water extending north and south of the chain of islands, on the west there is a shallower opening continuous with a large area of lesser depths comprising the greater part of Polynesia. To the southwest are two large shallow areas including respectively the Marshall and Caroline Islands, presumably the remains of much larger sunken land-masses. A chain of similar but

smaller shallows extends to the Malay Archipelago, and it is possible, at least, that this indicates the line of connections between Hawaii and the lands in the Southern Pacific.

As to the period at which Hawaii became completely isolated, it could hardly have been earlier than the Upper Cretaceous or early Tertiary, since, so far as we know, few of the modern angiosperms existed prior to the Upper Cretaceous.

The discovery of the Hawaiian Islands is usually credited to Cook, although it is not unlikely that some of the early Spanish voyagers may have touched at the islands. Cook first landed in 1778, and again a year later, when he was killed by the natives. In 1792–94, Vancouver visited Hawaii, and collections of plants were made, and in 1816, Kotzebue also visited the islands and collections were made by Chamisso (13), who also collected along the American coast and who discovered and named the Californian poppy, Eschscholtzia.

From the first settlement by Americans, in 1820, the study of the native flora has been encouraged and many important contributions have been made. In 1888 was published a comprehensive flora by Dr. William Hillebrand (25), who spent some twenty years in the Islands. This flora described 705 species of indigenous flowering plants, and 155 pteridophytes. Many additions have been made since the publication of Hillebrand's flora.

My first visit to Hawaii was in 1892. I was especially occupied in collecting material of the tropical pteridophytes and liverworts for a work on the archegoniates upon which I was then engaged, and comparatively little attention was paid to the higher plants. Some years later, during which time I had collected in the East Indies, the Islands were again visited, and I noted the occurrence of a number of liverworts apparently identical with Malayan species. Especially striking was the abundance of a conspicuous species, *Wiesnerella denudata*, indistinguishable from specimens collected by me in Java, and known elsewhere, except for Hawaii, only in northern India and Japan.

About this time, my attention was directed to the studies of Dr. H. A. Pilsbry of Philadelphia, on the land snails which are such a notable element in the Hawaiian fauna (34). Pilsbry states that these are very old types, now mainly restricted to Polynesia, but related to species of the adjacent Asiatic regions. Pilsbry believes that these primitive snails are relicts of an ancient fauna which have survived from a period when Hawaii was part of a continental area connected with the Polynesian area to the southwest. He thinks it impossible that these snails could have reached the islands from without, whether by birds or drift, or any other agency, since some of these agents would also have introduced some of the modern snails or slugs, none of which are known to be indigenous.

This at once suggested to me that the liverworts might offer a similar problem, and it seemed worth while to see how far the flora as a whole confirmed Pilsbry's conclusions. The result of this investigation was rather surprising. It was evident that a very large majority of the flowering plants were clearly related to the floras of the Southern Pacific, including New Zealand, Australia and the Malayan countries, while the American relationships were relatively few. These facts strongly supported Pilsbry's conclusions as to some more or less direct connections which once existed between the Hawaiian Islands and some much more extensive land areas to the southwest.

BOTANICAL REGIONS

The plant-formations in the islands are of several well marked types. Rock (35), who has given a very satisfactory account of these, recognizes six principal formations: 1. Strand flora; 2. Lowland; 3. Lower forest; 4. Middle forest; 5. Bog region; 6. Upper forest.

Strand Flora

Sandy beaches are not extensively developed, as the shore, especially in the more recent islands, is often composed of extensive recent lava flows, or steep broken cliffs, both unfavorable for the growth of maritime plants. This is true also for the beaches covered with broken lava boulders and pebbles. In the older islands, like Oahu and Kauai, there are beaches of coral sand, like the famous beach of Waikiki.

The strand flora is much less developed than in most tropical islands like those of the South Seas and West Indies. As in the East Indies, a conspicuous small tree is a screw-pine (*Pandanus odoratissimus*). Another small tree, found on most tropical beaches, is the "Hau" (*Hibiscus tiliaceus*). Other characteristic trees are *Calophyllum Inophyllum* and *Terminalia catappa*, also cosmopolitan strand species. Other cosmopolitan strand plants are *Ipomoea pes-caprae*, and *Scaevola frutescens*. A number of other wide spread species might be added—e.g., *Heliotropium curassavicum*, *Ruppia maritima*, *Scirpus maritimus*, etc. With these are some endemic species which are, however, usually somewhat local in their distribution. Such are two species of Schiedea, (Caryophyllaceae) and Brighamia (Lobeliaceae).

None of the trees and shrubs of the strand region are confined to it, and the line between the strand and the lowland above it is not at all clearly marked, many strand plants invading the lowland area, and *vice versa*.

Lowland Zone

On the lee side of the islands the lowland area is mostly open grassland, but even where it is not under cultivation, it has been invaded by introduced trees, especially in the neighborhood of Honolulu. The Algaroba, already referred to, and *Acacia farnesiana*, are perhaps the commonest. Fringing the beach near Waikiki, the groves of Casuarina recall the beaches of the East Indies, where it is one of the commonest strand trees.

According to Rock the most abundant of the native lowland grasses are *Andropogon contortus* and *Panicum torridum;* but many alien weeds have largely ousted the indigenous plants. In the dryer places the prickly pear (*Opuntia tuna*) has taken possession, and also lantana, both escapes from cultivation. The latter, however, is by no means confined to the lowlands, but has spread over the forested areas, up to 3,000 feet or more. The Mexican poppy, *Argemone* (sp. ?) is a showy plant of the lowlands.

Lower Forest

This extends up to 2,000 feet elevation. There is naturally a marked difference in the character of the forest on the windward and lee sides of the islands. On the windward side of Hawaii, for example, the steep cliffs are forested to the water's edge, and there is a typical rain-forest of great luxuriance, but less rich in species than the dryer lee forest.

Two trees, possibly not truly indigenous, are the most numerous in the lower forest. Approaching Honolulu from the sea, the eye is at once arrested by patches of pale green in the dark green forest mass

covering the base of the mountains. This light green foliage belongs to the "Kukui"—*Aleurites moluccana*, which with the "Ohia" *Jambosa malaccensis*, make up a considerable part of the lower forest. Associated with these are many endemic shrubs and trees. One of the most important of these is "Koa," *Acacia koa;* others are species of Straussia, Gardenia, Bobea, Sandal wood (Santalum) Pisonia, and others. Also, but more abundant at higher elevations, is the "Ohia lehua," *Metrosideros polymorpha*, perhaps the most wide spread of the Hawaiian trees.

The lower forest on the leeward side is quite different in character. The soil is usually more or less arid, and there is a scanty undergrowth, and a marked scarcity of lianas and epiphytes. Of the former are species of Caesalpinia, Cocculus and Sicyos. Two parasites are common, a mistletoe, *Viscum articulatum*, and *Cassytha filiformis*.

There are many more species in this dry forest, and among these are some of the most characteristic Hawaiian genera. The Araliaceae, e.g., Reynoldsia, Tetraplasandra, Cheirodendron, notable features of the Hawaiian flora, are especially developed in this lowland forest. A very common tree is the liliaceous *Dracaena aurea*, which resembles a tree Yucca, or the New Zealand *Cordyline australis*, often planted in California.

A few of the trees shed their leaves during the dry season but most of them are evergreen. One of the commonest deciduous trees is *Erythrina monosperma*.

The species of the mixed lowland forest are for the most part the same in all the islands, but there are a good many local species, often of very limited range.

The Middle Forest

The lower forest merges gradually into the middle forest zone, which extends to about 5,000 feet elevation. This zone is for the most part a pronounced rain-forest and in the windward areas receives an enormous rainfall. In this wet forest the vegetation reaches its maximum luxuriance.

In the mountains back of Honolulu are several valleys in which there still may be found a considerable amount of forest. As the mountain range is only about 3,000 feet high, the rain winds pass over the summit and heavy rains are deposited in the valleys. It may be as much as 200 inches annually while a few miles away, in the coastal area, it is less than one-fourth as much.

McCaughey (27) has given a good account of the vegetation of Mauoa, the largest of these valleys. Most of the lower forest has disappeared, but the head of the valley still harbors much of the original forest.

Where the lower forest still exists it is composed mainly of Kukui (Aleurites) and Ohia (Jambosa). Above the Kukui zone is a region characterized by another important native tree, *Acacia koa*, allied to the phyllodineous Australian species. Above the Koa zone is the rain-forest in which are found many characteristic, mainly endemic, trees and shrubs. Among these are species of Antidesma, Cheirodendron, Eugenia, Ilex, Hesperomannia, Metrosideros, Osmanthus, Pelea, Pittosporum, Santalum, Pritchardia, Suttonia, Cyanea, Coprosma, Hibiscus and others. This wet forest abounds in liverworts, mosses and ferns.

While some species like *Acacia koa* and *Metrosideros polymorpha*, occur in all the islands, each of the larger islands has many species peculiar to it. The percentage of these endemic species increases with the age of the islands, and attains its maximum in Kauai. The latter is therefore, of especial interest to the botanist.

The greater part of this island is occupied by a plateau of about 4,000 feet elevation, rising in the center to 5,000 feet in Mt. Waialeale. This mountain receives the extraordinary rainfall of about 500 inches annually.

The ascent from the lowland to the plateau is very abrupt. The enormous precipitation in the center of the island has resulted in the erosion of several deep canyons cutting into the table land. The writer visited one of these, the Olekele canyon, whose steep walls were clothed with luxuriant vegetation, including many liverworts and ferns. The most interesting plant noted was a begonia, *Hillebrandia sandwicensis*, the only member of the family known from Polynesia.

At the edge of the plateau is a fine open forest in which Metrosideros is the predominant tree; but as one penetrates to the center of the island, the moisture increases rapidly, and the ground becomes a bog, into which one sinks at every step. The carpet of mosses and herbaceous plants finally is replaced by an open bog with a few stunted shrubs and trees, and tussocks of coarse grasses and sedges.

Rock (35) has given a detailed account of the middle forest of Kauai, which is probably the richest in species of any in the whole Archipelago.

As we have already stated, the predominant tree of the marginal area is Metrosideros, with some *Acacia koa*, which belongs rather to the lower forest zone. Associated with Metrosideros are *Sideroxylon sandwicensis*, *Tetraplasandra waiemeae* and *Cryptocarya mannii*. Among other characteristic forms are species of Santalum, Elaeocarpus and Pittosporum.

Toward the interior of the plateau other trees become dominant, among them the Araliaceous genus Cheirodendron, and several Rubiaceae belonging to endemic genera, e.g., Kadua, Gouldia, and another endemic genus, Pelea (Rutaceae), most of whose species are restricted to Kauai. The ground in this region is saturated and the trees and shrubs are covered with a thick blanket of mosses and liverworts in great variety, and support many epiphytes, especially ferns. Among these are numerous beautiful filmy ferns (Hymenophyllaceae).

Besides the trees, many characteristic shrubs and herbaceous plants grow in this rain forest. Several endemic genera of Compositae, Dubautia, Raillardia, Wilkesia; two Liliaceae, Astelia and Dianella, also found in the Australasian regions, are common, but perhaps most notable of the plants of this region are the numerous species of Lobeliaceae, which reach an extraordinary development in the Hawaiian Islands. Unlike the low growing herbaceous species of the United States, some of the Hawaiian forms are 20–30 feet high, or occasionally more. These giant lobelias (Cyanea) have tall slender trunks with a crown of gigantic leaves, giving the plant something the aspect of a palm. The Lobeliaceae are especially abundant and varied in Kauai.

In the wet forests on all the larger islands, one may encounter one of the most remarkable of the Hawaiian plants, *Gunnera petaloidea*, which resembles a gigantic rhubarb, the huge peltate leaves being four or five feet in diameter.

The native palms of Hawaii all belong to the genus Pritchardia, with about ten species distributed throughout the islands, but not abundant as individuals.

Climbing plants are relatively scarce. The most conspicuous is *Freycinetia Arnotti* (Pandanaceae) which is very abundant and when in flower is rather showy, due to the red bracts of the inflorescence—but the most striking of the native climbers is the leguminous *Strongylodon lucidum*, with vivid scarlet flowers beloved of the honey-sucking birds.

There is, in general, a marked scarcity

of showy flowers among the native plants. Most conspicuous is the ubiquitous *Metrosideros polymorpha*, whose masses of crimson flowers are very showy. Some of the lobelias have rather attractive flowers, and occasionally a native Hibiscus with white, pink, or yellow flowers is encountered. Species of Cyrtandra and Scaevola, the former a genus abundant in the Malayan Islands, also have attractive flowers.

As in all volcanic islands ferns play an important rôle in the Hawaiian flora. They reach their maximum development in the rain-forest, where tree-ferns, (*Cibotium spp.*) reach a large size. While the majority of species belong to the great family Polypodiaceae, all of the families, except the Osmundaceae, are represented. In the rain-forest, often epiphytic upon the stems of tree-ferns, are several species of Hymenophyllum and Trichomanes. The curious *Ophioglossum pendulum* and the stately *Marattia Douglasii* represent the Ophioglossaceae and Marattiaceae.

In the dryer lowlands, *Gleichenia linearis*, a cosmopolitan species, forms impenetrable thickets, and on the recent lava flows ferns are among the earliest plants to gain a foothold. Among these the peculiar Hawaiian genus, Sadleria, is conspicuous.

The Upper Forest

Rock has made a special study of the upper forest on the lofty volcanoes of Maui and Hawaii. On Mauna Kea, in Hawaii, this forest reaches 11,500 feet elevation. It consists of four dominant species, the most abundant being *Sophora chrysophylla* and *Myoporum sandwicense*. With these in the lower areas are the ubiquitous Koa and Metrosideros. *Sophora chrysophylla* is one of the numerous Hawaiian species whose nearest relatives are found in New Zealand. The New Zealand species is so close to the Chilean *S. tetrapteris*, that it is by some botanists considered to be identical. Arborescent Compositae, *Raillardia arborescens* and *R. struthioloides* are an important element at the upper limits of the forest.

Bogs

The bogs found at elevations of 4,000–5,000 feet are characteristic features of the Hawaiian flora. Such bogs are found on the elevated plateaus of the older formations, as in Kauai, West Maui, and the Kohala mountains of Hawaii. The extensive bogs about Mt. Waialeale in Kauai afford excellent examples of such formations, which are reminiscent of the peat-bogs of the north temperate zone. The precipitation in Waialeale is enormous, approximating 500 inches annually, and the whole region is almost constantly covered with clouds.

The soil is saturated, and decayed vegetation may be found ten or fifteen feet below the surface. Sphagnum occurs in places, but for the most part the bog is covered with tussocks of coarse grasses and sedges. Two bunch-grasses—*Panicum monticola* and *P. isachnoides*—are abundant and in these tussocks two lycopods grow—*Selaginella deflexa* and *Lycopodium erubescens*. A most unexpected inhabitant of these bogs is a sundew, unknown elsewhere in the Islands, but apparently identical with *Drosera longifolia* of Northern Europe and America. Rock mentions among other characteristic plants a handsome blue violet and an orchid, *Habenaria holochila*, one of the four known orchids of Hawaii. Coarse sedges, including species of Carex, Rhynchospora and Oreobolus, are abundant. The latter is a genus characteristic of sub-antarctic America and New Zealand, and this is also the case with Astelia, a liliaceous genus. In this boggy region are a number of such temperate genera as Rubus, Vaccinium, Viola, Geranium. "Creeping forms of woody Metrosideros, Cyathodes, Geranium, Lysimachia, and a

number of rare, mostly single representatives of genera, which have their home in Antarctic (sic) regions of New Zealand, the Falkland Islands, and Southern Andes." (25, XXIV.)

Lava Flows

In all of the older regions volcanic activity has long since ceased, and the lava is more or less completely disintegrated. Hawaii, however, with its two great active craters, offers exceptional opportunity for studying the effects of the eruptions upon the vegetation, the invasion of the lava by various plants, and the establishment of new plant associations.

The frequent eruptions of Mauna Loa, with extensive lava flows down its slopes, sometimes reaching the sea, have resulted in the complete destruction of the vegetation over large areas.

Where the precipitation is light as on the lee side of Hawaii, the lava is little affected by exposure to the atmosphere, and much of the leeward or "Kona" side of the island is a desert of dead lava. Rock (35) mentions three lava flows in the Kahuku district which after an interval of fifty years showed no noticeable alteration.

Much the same conditions are found in the great crater of Haleakala, in Maui. Although there is no record of eruptions there is every evidence that activity ceased in relatively recent times, and the lava flows on the floor of the crater, protected by its lofty walls, show no signs of disintegration.

In the regions of heavy rainfall plants soon obtain a foothold on the lava and new soil is produced. It is probable that like the new flora of Krakatau (40), the first plants to settle on the lava are blue-green algae, and as in Krakatau, pteridophytes play an important rôle in the colonizing of the fresh volcanic soils. The writer in 1919 visited a great lava flow, which in 1881 threatened to destroy Hilo, the principal city of Hawaii. The great expanse of lava was easily recognizable, although it was covered with the beginnings of a new forest. Various pteridophytes were abundant, with a variety of ferns, among them the characteristic *Sadleria cyatheoides*, which seems to be one of the first to establish itself. Species of Lycopodium and Psilotium were also noted.

The most important element of the embryo forest was the ubiquitous *Metrosideros polymorpha*, which seems always to appear upon the recent lava. In the rain-forest this tree commonly begins its career as an epiphyte, especially on tree-ferns, where it often develops stilt-roots like those of so many species of Ficus.

Dr. H. L. Lyon, of Honolulu, who accompanied me on this occasion, informed me that practically all colonists on the new lava were strictly indigenous species. The introduced plants, such as the common weeds of this vicinity, failed to obtain a foothold.

Sometimes the forest on an elevation escapes the encroaching lava and forms more or less extensive islands in the surrounding lava flow. These islands, or "Kapukas" may give a clue to the vegetation which had occupied the region before the invasion of the lava. Rock gives an interesting description of one of these Kapukas, 56 acres in extent, near the great crater of Kilauea. "This little oasis shows no sign of lava rock but has rich, deep black soil which supports a marvelous mixture of vegetation. As many as forty species of trees are present in this beautiful park-like spot." It is gratifying to know that this is now included in the Volcano National Park.

When the writer first visited the volcano in 1892, the greater part of the road from

Hilo was through dense unspoiled rain-forest. In 1919 the lower forest, up to about 2,000 feet elevation had given way to cane-fields. Above this most of the forest along the volcano road had been cut down, or so ravaged by cattle and the consequent encroachments of Hilo grass and other weeds, that very little had survived. The last forlorn stragglers of the groves of tree-ferns that formerly lined the road were slowly dying, exposed to sun and wind, and skeletons of dead trees rose from a waste of tangled weeds and grass.

THE AFFINITIES OF THE HAWAIIAN FLORA

The remarkable richness of the flora, and the extraordinary degree of endemism has already been referred to, and this is especially true of the flowering plants.

Undoubtedly the aboriginal immigrants introduced a considerable number of plants that have become naturalized. The staple food plant, "taro" (*Caloçasia antiquorum*) bread-fruit, banana and coconut probably all reached the country through human agency, and it is not unlikely that the Kukui (Aleurites) and Ohia (Jambosa), which now form forests all over the territory, may also have been thus introduced, as they are important economic plants found throughout Polynesia. Other species could be mentioned, e.g. *Cordia subcordata*, which are perhaps in the same category.

The botanist is at once struck with the preponderance of Old World genera among the trees and shrubs of the Hawaiian forest. The great majority which do not belong to endemic genera, are members of extra-American genera belonging to Australasia, or the East Indian regions. The commonest tree of the middle forest is *Metrosideros polymorpha*, a species found also in New Zealand, and throughout Polynesia. *Acacia Koa*, also extremely abundant, is of the phyllodineous type, especially characteristic of Australia. Pandanus and Freycinetia represent the exclusively Old World family Pandanaceae. The only genus of palms, Pritchardia, is confined to Polynesia. Other examples of familiar Old World genera are Pittosporum, Gardenia, Santalum and Dracaena.

Contrasted with these is the complete absence of any of the characteristic trees and shrubs of North America. Not only are there no conifers, but such universally distributed types as oaks, willows, poplars, maples, roses and a multitude of others, are conspicuous by their absence.

A marked feature of the Hawaiian flora is the complete absence of conifers, which are wanting throughout Polynesia. There are other forms which might be expected, but are either absent or very poorly represented. The wide spread genus Ficus is entirely wanting, and the important family Araceae has no certainly indigenous representatives. The scarcity of orchids is most remarkable. This, the largest family of flowering plants, with 17,000 species distributed over practically the whole world, is represented in Hawaii by but four species. There are no truly native Scitamineae, although species of Musa, Zingiber, Canna and Hedychium are completely naturalized.

Of the non-endemic genera, a few are cosmopolitan, like many grasses and sedges, Ranunculus, Lepidium, Silene, Geranium, Hibiscus; but the great majority belong to the South Pacific and the adjacent Malayan regions.

While Australia and New Zealand share with the Malayan region many genera and a good many species, there are certain genera, and even families, which are essentially Australian, and others which reach their maximum development in New Zealand. While Australia and New Zea-

land are often united as Australasia, they differ very much more in their floras than is generally supposed. In New Zealand especially, there is a considerable number of species which are closely related to, or identical with South American types. This "sub-antarctic" or "Fuegian" flora is also represented to some extent in the cooler and moister regions of Southeastern Australia, and has also some representatives in Hawaii. Examples of these are Astelia, Oreobolus, Nertera and Sophora. The latter has already been referred to. The geographical distribution of *Nertera depressa* is very remarkable. It is a pretty little trailing plant with scarlet berries, somewhat suggestive of the partridge berry (Mitchella), which belongs to the same family. Its range is along the Andes from Mexico to Tierra del Fuego, and it is common in New Zealand and Australia. It is reported also from the mountains of Tahiti. A similar, possibly identical species occurs in the higher mountains of the Malay Archipelago, as far north as the Philippines. The majority of the species are in New Zealand, which would appear to be the headquarters of the genus.

About fifty extra-American genera are common to Hawaii and the Australasian-Malayan region while the peculiarly American-Hawaiian genera number a scant half dozen (9).

An analysis of the Australasian flora, aside from the Fuegian element, shows two fairly distinct categories. In eastern and northeastern Australia and throughout New Zealand, the vegetation is markedly Malayan in type, and there is abundant evidence that both countries had former connections with the Malayan regions to the north, from which were derived, probably independently, many related or identical species. Some of these are shared with Hawaii, where such genera as Pandanus, Gardenia, Cyrtandra, may be considered as Malayan, rather than Australian.

The second element is the large and peculiar autochthonous flora of Australia, scantily represented elsewhere, and poorly developed in New Zealand. The latter, however, has a considerable number of dominant genera, some of them endemic, and a large proportion of endemic species.

Among the Hawaiian genera which have their greatest development in Australia are the following: Acacia, Byronia, Cassytha, Cyathodes, Dianella, Dodonaea, Exocarpus, Gahnia, Myoporum, Pseudomorus, Santalum, Scaevola, Vittadinia. In several of these, the majority of the species, outside Australia, are found in Hawaii. Scaevola is a good example of this. It belongs to the family Goodeniaceae which has many representatives in Australia but few elsewhere. According to Hillebrand (25), outside of Hawaii, which has eight endemic species, aside from the widespread *S. Lobelia*, only a single species, from New Caledonia, is known, while over fifty are found in Australia (12).

The relationships of the Hawaiian flora with that of New Zealand are very evident. The following characteristic New Zealand genera are well represented in Hawaii: Acaena, Astelia, Baumea, Coprosma, Gunnera, Metrosideros, Myrsine, Nertera, Oreobolus, Pittosporum, Sophora (*section* Edwardsia). Some of these, like Gunnera and Astelia, are shared with subantarctic South America. Coprosma, familiar to Californians through the extensively planted *C. Baueri*, is especially interesting, since of about forty known species, twenty-seven are found in New Zealand and nine in Hawaii.

Among the most remarkable plants of Hawaii is *Gunnera petaloidea*, already referred to, found in the wettest mountain

forests. Its gigantic leaves are much like those of the Chilean species sometimes seen in cultivation. The genus reaches its greatest development in the Andes and sub-antarctic South America and New Zealand. A single species occurs in the mountains of Java and in the Philippines, and it may be that the Hawaiian species is more nearly related to the Malayan species than to those of New Zealand.

As might be expected from the extreme isolation of Hawaii, not only is the proportion of endemic species very high, but there are many endemic genera as well. Some of these show more or less evident relationship with Australasian genera. The Hawaiian lobeliaceous Brighamia may be compared with the Australian Isotoma, Tetramalopium (Compositae) with Vittadinia, Pelea (Rutaceae) with Melicope, and Cheirodendron (Araliaceae) with the New Zealand Pseudopanax (25).

The Hawaiian Araliaceae are especially interesting, and show certain parallelisms with those of New Zealand. Of the five genera recognized by Hillebrand, three are endemic, and of the other two Reynoldsia is confined to Polynesia, and Tetraplasandra, with two endemic Hawaiian species, has a third species in New Guinea and the Sunda Islands. The endemic Hawaiian Cheirodendron is said to be close to the New Zealand Pseudopanax. Hawaii has four genera and fifteen species compared with six genera and seventeen species in New Zealand; while the whole United States has but three genera and eight species.

While the American element in the Hawaiian flora is much less evident than the types allied to those in the southern hemisphere, there are a good many species whose American relationships are unmistakable. These are mostly related to forms found on the American Pacific coast. The wild strawberry, *Fragaria Chilensis*, is identical with the American species, and the genus Sisyrynchium, except for the solitary Hawaiian species, is confined to America. Most of the very characteristic endemic genera of Compositae also have their nearest relations among the Western American types. Thus Campylotheca is close to Bidens and Coreopsis; Argyroxiphium, the "silver sword," and the closely allied Dubautia, are related to the Californian tar-weeds, Madieae, and the Hawaiian Raillardia is close to the Californian Raillardella.

A small number of other genera, e.g. Nama, Vallesia, are also apparently of American origin, but seem to be characteristic of South America rather than of Western North America.

Perhaps the most interesting family from the standpoint of evolution is the Lobeliaceae with over a hundred species. A small number of these are species of the cosmopolitan genus Lobelia, but the rest belong to five endemic genera of which the most important are Clermontia and Cyanea, and these show the most remarkable developments. Some of them assume tree-like dimensions, occasionally 30–40 feet in height. The slender trunk is often unbranched, and terminates in a palm-like crown of huge lanceolate leaves, beneath which are clusters of curious flowers.

Rock (36), who has made a special study of the family, states that nowhere except in South America, is the family so wonderfully developed. In South America the family is especially represented in the Andes and in Brazil. The extraordinary number of Hawaiian species is especially remarkable, as only four species are known in Polynesia, restricted to Tahiti and the neighboring islands of the Society group.

Pteridophytes

Hillebrand (25) lists 155 species of pteridophytes of which seventy-nine are endemic. As in all countries, a large majority of the species belong to the Polypodiaceae. The most primitive families, Marattiaceae and Ophioglossaceae, are represented by three species of Ophioglossum and one each of Marattia and Botrychium.

Ophioglossum pendulum is widespread through the Eastern tropics, and also occurs in southern Polynesia. The Hawaiian plants were smaller than specimens collected by the writer in Ceylon and Java, but otherwise identical. The single species of Botrychium is endemic, and Christensen (15) considers *Marattia Douglasii* as also truly endemic. A single species of Schizaea, *S. robusta*, also found in Tahiti, is the sole representative of the family Schizaeaceae. Five species of Trichomanes, three endemic, and four of Hymenophyllum, only one of which is known elsewhere, represent the filmy ferns, Hymenophyllaceae. One species, *Trichomanes parvulum*, whose tiny fronds are hardly half an inch in length, is found throughout the Eastern tropics, and also in the larger Polynesian islands.

Of the Gleicheniaceae, one species is endemic. The cosmopolitan *Gleichenia linearis* (*G. dichotoma*), is extremely abundant, and *G. longissima*, a common Asiatic and Malayan species, occurs in many parts of the islands.

The tree-ferns are all endemic species of Cibotium. *Marsilia villosa*, apparently most nearly related to the West American *M. vestita* is the only representative of the Hydropterides.

The widespread *Psilotum triquetrum* and *P. complanatum* are common, and Hillebrand lists ten species of Lycopodium, six endemic, and five of Selaginella, with three peculiar species.

Of the non-endemic species, aside from the cosmopolitan ones, the great majority are either Australasian or Malayan. The only American species, viz. *Asplenium fragile* and *Pellaea ternifolia*, are Andean species which reach Mexico and Texas.

A recent list of the Hawaiian Pteridophyta (15) lists 159 species, of which about 100 are considered to be endemic.

Bryophytes

Hepaticae

The writer has collected liverworts in Hawaii, where they are very abundant, especially in the wet mountain forests. Perhaps the most conspicuous and one of the commonest is *Dumortiera trichocephala*, a species occurring throughout the Indo-Malayan regions, but which is absent from the American tropics, where it is replaced by the cosmopolitan *D. hirsuta*, also found in Hawaii.

Often associated with Dumortiera is another conspicuous liverwort, *Wiesnerella denudata*, a monotypic species, known elsewhere only from Java, the Himalayas and Japan. Both of these characteristic Asiatic species inhabit wet shady localities, often on dripping rocks along streams. They would hardly seem to be adapted to dispersal over wide land areas, let alone such expanses of ocean as separate Hawaii and the Southern Pacific.

Other characteristic liverworts are the Anthocerotaceae, which are probably very old and primitive forms. They also are characteristic of the rain-forest. One genus, Dendrocesos, is epiphytic, the plants of extreme delicacy. The thin-walled green spores germinate immediately on ripening, and would probably be quickly killed by even short exposure to

the heat and dryness of the open lowlands, and this probably is the case with most of the liverworts, so that it is scarcely likely that these could have been brought to the islands by wind or water transport (6).

Stephani's Index Hepaticarum (38) shows that aside from the endemic and cosmopolitan species, the Hawaiian liverworts are almost exclusively species belonging to Southern Polynesia, Australasia and Indo-Malaya. There are only two American species which do not also belong to the Old World.

The only likely means of transport for the spores of most species would seem to be in mud adhering to the feet of rapid flying migratory birds. As there are, at present, no migrants from the South Pacific, not to mention the great distance of the nearest source of supply, it is doubtful whether this will explain the presence of so many Asiatic and Australasian types. It is possible that some of the wide ranging sea birds might reach Hawaii from the Southern Pacific, but it is highly improbable that they would carry spores from plants living in the depths of the mountain forests.

In this connection we might note an interesting case. A Hawaiian liverwort, *Lepidozia sandwicensis*, is said to occur also in Alaska. The most common migratory bird of the islands, the golden plover, regularly migrates in large flocks from Alaska. It may well be that this bird was the means of carrying this liverwort to Alaska. As there are a number of other bird migrants from the Western American coast, it is highly probable that through these, such immigrants as the wild strawberry and other American types have reached Hawaii. As all the known migratory birds are American, they could hardly have played a rôle in the transportation of species from the South Seas.

From the data at hand, therefore, it is clear that the hepatic flora of Hawaii is closely related to that of the South Pacific regions, and southeastern Asia.

Mosses

From a recent list of the Hawaiian mosses (3) it is evident that much the same conditions exist as in the Hepaticae. The great majority are endemic, and where a species occurs outside Hawaii, it in nearly all cases belongs to the South Pacific or to the Malayan-Asiatic regions. An example of such distribution is *Thysanomitrium blumii*, which is found in Southern India, Ceylon, Sumatra, Java, Celebes, Borneo, Philippines, Formosa, Japan and Polynesia. More restricted in range is *Leucobryum hollianum*, recorded outside Hawaii only from Java and Borneo.

Algae and Fungi

The algae and fungi are too imperfectly known to afford an entirely satisfactory comparison with other regions. McCaughey has published a list of algae showing a good many cosmopolitan species, and a considerable proportion of endemics. Of the non-endemic, but not cosmopolitan species, the majority appear to be related to those of the South Pacific and Indian Ocean.

Stevens (39) has published an important list of the Hawaiian Fungi, but it is devoted mainly to parasitic forms. The larger fleshy fungi are still very imperfectly known.

As in the flowering plants, there is a high degree of endemism. Of one characteristic genus, Meliola, Stevens says, ". . . . all the Meliolas collected in Hawaii are found on plants indigenous to

the islands, and most of the host species are endemic with large representation of such typically Hawaiian genera as Gouldia, Clermontia, Kadua, Lobelia, Pelea, Scaevola, Straussia."

He recognizes the close relationships of these host plants with those of the South Seas, and concludes that the parasites must also have come from those regions. He thinks the Meliola flora is much older than the rust flora (Uredinales). "This relation of the Meliolas to the ancient flora of the islands clearly points to their long, even very ancient, association with these hosts or their progenitors."

Hillebrand, in the introduction to his Flora, considers at some length the problems of the origin of the Hawaiian plants. He was convinced that the archipelago has always been completely isolated, and that it has received all of its flora from outside. He believed that oceanic currents were the agents of transport, and especially the equatorial currents. He does not, however, explain how the seeds, spores, or fruits, of delicate forest plants, could have survived the long voyage from the South Seas to Hawaii.

This view of the complete isolation of the islands, from their first formation, was maintained for a long time, and the most comprehensive attempt to explain the origin and distribution of the flora on this theory, was offered by Guppy (24). His views as to the advent of the various elements of the flora are exceedingly ingenious and suggestive, but his conclusions cannot always be accepted without question.

Guppy believes that the islands first appeared above the ocean in early Tertiary time, and that the establishment of the vegetation followed the same course as that of the new flora of Krakatau after the great eruption of 1883. The conditions in the two cases are very different, however, although there is a certain apparent similarity.

Krakatau is less than fifty miles distant from Java and Sumatra, with their extremely rich and luxuriant vegetation, whence in less than twenty-five years, as the writer can testify from a visit in 1906 (7, 19), the devastated island was completely covered with abundant and varied plant growth. A comparison of Krakatau with Hawaii, over 2,000 miles away from the nearest mainland, and still more remote from the nearest habitat of most of its genera, is justifiable only to a very limited degree.

Guppy assumes that as in Krakatau the first immigrants were simple algae, mosses and ferns, carried by the wind. It is true that the spores of many ferns are well fitted for air transport, and the wide distribution of some species, like the common bracken fern, may be due to this. But some ferns, like Osmunda and the Hymenophyllaceae, are quite unfitted for wind transport over long distances, as their delicate green spores quickly lose their viability. It is hardly likely then that the filmy ferns of Hawaii could thus have reached the islands from New Zealand or the Malay Archipelago. The fact that nearly all the Hymenophyllaceae are endemic indicates that they belong to the ancient flora.

Guppy thinks the peculiar Compositae were among the earliest immigrants, antedating the influx of plants from the southern hemisphere which are now predominant. He recognizes the evident relationships with American types, and thinks they were transported by birds. This latter theory may be correct—but it probably was at a relatively late period, and not in the early Tertiary, as Guppy believes. At that time the highly special-

ized and relatively modern Compositae of California, e.g. Madia, Raillardella, could hardly have existed, and these are believed to be the nearest living relatives of the specialized Hawaiian Compositae. It seems much more likely that this composite element is relatively modern, and not a remnant of the primary flora. The geological history of California is such as to indicate that most of its numerous and peculiar Compositae are comparatively recent developments.

The Lobeliaceae are also regarded by Guppy as being, like the Compositae, of American origin, but this relationship is by no means so evident as in the case of the Compositae. The Lobeliaceae are also considered by Guppy to belong to the very early flora of Hawaii.

The predominant Malayan and Australasian types are thought to have come in at a later period. These plants Guppy believes were introduced through the agency of birds, especially fruit-eating pigeons. He assumes that at some former period there was a very active dispersal of plants in the Pacific Islands through birds, whose activity later, for some unexplained reason, ceased.

To believe that such plants as Gunnera, and many other inhabitants of the mountain rain-forests, could have been carried from New Zealand or Chile to Hawaii, is certainly a strain on the imagination.

Another difficulty in this connection is the present bird fauna of Hawaii. Aside from a number of American migratory shore birds and waterfowl, practically all the birds are peculiar to the islands, and the great majority belong to a single very specialized family, Drepanididae, whose relationships are problematical. Wallace (41) considers them most nearly related to the flower-peckers (Dicaeadae) of the Old World tropics. None of these birds could have been responsible for the introduction of the numerous South Pacific plants, and if these owe their introduction to bird agency, it seems strange that none of the birds responsible for these introductions should have left descendants in Hawaii. According to Guppy's hypothesis, these birds were fairly numerous, and not merely occasional stragglers, and it would be hard to explain the complete absence of such birds from the present fauna.

The strand flora of Hawaii is notably poor in species when compared with most tropical regions. The principal ocean drift at present is from the northeast, but the likelihood of many species from the Northern American coast, which might have drifted to Hawaii, becoming established in such a different climate, is not great. It is quite likely that such widespread species as *Ipomoea pes-caprae*, Scaevola, *Hibiscus tiliaceus*, may have been drifted to the islands from the south, as many strand plants have special adaptations for water transport.

It is quite likely that some species have been introduced through the agency of wind. This may be the case in some ferns, and it is not impossible that some of the Compositae may have thus reached Hawaii from Western America.

The small number of American types is remarkable inasmuch as there are agencies which might be expected to bring to the islands a good many plant immigrants. A considerable number of birds are regular migrants from the American coast, and the prevailing trade winds are from the same direction. Moreover, ocean currents frequently bring drift from Northwest American shores. None of these agencies, however, can account for the transfer of seeds from the remote regions to the south, whence it is certain most of the plant life of Hawaii has been derived.

While recognizing the difficulties in-

volved in attempting to explain the derivation of the existing Hawaiian flora, the evidence offered by the advocates of the theory of the strictly oceanic origin of the Archipelago is by no means adequate, as it involves assumptions, such as the extraordinary rôle of birds in seed-distribution, which are, to say the least, quite incapable of satisfactory proof.

The evidence for a former more or less direct connection with New Zealand, Australia and the Malay Archipelago, is fairly strong; and the admission of such communications will readily explain most of the difficulties involved in the theory that the Archipelago has always been completely isolated.

We may assume that the Hawaiian Archipelago, as it now exists, is but a remnant of a much larger land-mass which has been in subsidence for a long period, and that extensive subsidence has also occurred throughout Polynesia, and to a lesser degree in Australasia. One argument for this assumption is the great development of coral reefs in the Pacific, especially in Polynesia and northeastern Australia. The existence of active coral reefs involves continuous subsidence (17) and the absence of large land masses in mid-Pacific, with the innumerable small coral islands and reefs, can be explained most satisfactorily on the theory that the latter are the remnants of submerged land-masses of large size—possibly even of continental dimensions.

It is known that the Malay Archipelago was once united with the Asiatic mainland and that the southern extremity of the American continent was connected in some fashion with New Zealand. The remarkable similarity between the flora of Hawaii and these southern land-masses indicates, in the writer's judgment, that the present flora of Hawaii is in large part descended from types which were widely distributed over land areas which connected Hawaii with the ancient continents of the South Pacific. These ancestral types, in the course of ages, have become greatly altered in some cases, but others have persisted with little change. Presumably a good many forms have become extinct, and others have been introduced from outside since the isolation of the islands. In the latter category may probably be placed those Hawaiian species whose relations are evidently with those of the Pacific Coast of North America.

The objection has been brought against the continental theory of the Hawaiian Archipelago that certain types are absent, which on this theory we should expect to find. First in importance are such conifers as Araucaria, Agathis, and Podocarpus, characteristic genera of the Southern Pacific regions. Another notable case is the almost cosmopolitan genus Ficus. Another instance is the widespread family Araceae, with but two Hawaiian species, both almost certainly introduced by man. Other examples might be found, and these objections are valid ones, and not easy to explain.

The most probable explanation would be that some of these forms did exist, but have become extinct since the isolation of the islands. There are plenty of examples of plant extinction. We have but to recall the former wide distribution during the Tertiary of such now restricted genera as Sequoia, Taxodium or Liriodendron. Unfortunately there are no fossils to record the early history of the Hawaiian flora, and we can only conjecture what agencies may have caused the extinction of these missing types, supposing they did formerly exist. The most obvious explanation would be the extensive volcanic activity to which all the islands have been subjected, and whose destructive effects can be studied today in the

lava flows from Mauna Loa. Every region of the Archipelago has at some time been covered with lava, and it is not unreasonable to suppose that many species, especially those of local distribution, may have been destroyed as the direct result of volcanic eruptions.

An indirect result of the purely volcanic nature of the existing islands may have been a gradual extinction of species which require certain constituents absent from purely volcanic soils. The almost complete absence of granitic or calcareous soils, for example, might practically prevent the persistence of species present at an earlier period when areas existed which had not been covered by lava.

Another factor might also be considered, viz. the ravages of disease. Just as in large areas of the Eastern United States the chestnuts have been wiped out by the ravages of a fungus, so we may imagine species may have succumbed to similar enemies, and owing to the isolation of the Islands could not reestablish themselves.

We may conclude, then, that the bulk of the Hawaiian vegetation is made up of residual types, i.e. remnants of a flora common to the ancient much larger Hawaii, and the continental masses of the Southern Pacific and Malaysia. These ancient types have become more or less changed since the isolation of the Archipelago and their number has been augmented by a relatively small number of forms introduced from America subsequent to the isolation of the Islands.

FAUNA

The animals of Hawaii show the same predominant relationships with those of the South Pacific countries, only a small number of species indicating a derivation from American sources. This holds good for both vertebrate and invertebrate forms.

The subject of the land snails has already been referred to. Among the insects there is the same high degree of endemism, and the majority of species are related to Australasian and Indo-Malayan types (31).

In a former paper (9), the writer has given a statement of Professor W. K. Fisher of Stanford University, concerning some of the marine invertebrates of Hawaii. Professor Fisher says,

> In regard to the shallow-water and shore species of starfishes and holothurians which I have personally studied, the following general statement seems to apply: The starfishes are all tropical forms, and those which are not peculiar to the islands are chiefly Indo-Pacific, and comprise mostly wide-ranging species, some of which extend from the Red Sea to China and Japan, and thence to Australia. Considering the shallow-water species and those from moderate depths which are peculiar to the Hawaiian group, we find their nearest relatives in the Indian Ocean, East Indies, and north of Australia. In a few cases the same species from moderate depths, ranges into the East Indies as far as the Indian Ocean. Only one undoubted American starfish is found in Hawaii. There is no similarity in the faunas of the West Coast of America and the Hawaiian Islands.

The late Dr. D. S. Jordan also informed the writer that the shore fishes of Hawaii are related to those of the Southern Pacific and not to American types.

No indigenous Amphibia are known from Hawaii. This may possibly be explained by assuming that the islands were shut off at a period before that in which the modern amphibia, the toads and frogs, were developed. A similar condition obtains in New Zealand where only a single species is known.

About half a dozen lizards are known, all widespread species of the Southern Pacific region. It is probable that these were introduced with the early human immigrants or possibly may have reached the islands by drift.

With the exception of a single bat, the mammals probably all were introduced by human agencies.

Birds (33)

The birds of Hawaii are of extraordinary interest. Except for a comparatively small number of migratory species, wide-ranging sea birds and occasional stray visitors, all species are peculiar to the Archipelago. All of the passerine birds are endemic and mostly confined to the mountain forests.

Forty out of forty-nine species of passerine birds belong to a peculiar family, Drepanididae, confined to Hawaii, so specialized that their relationship with other birds is problematical. Wallace (41) thinks the family most nearly related to the flower-peckers, Dicaeadae, widely distributed through Australasia and the Old World tropics. Like the flower-peckers, their Hawaiian relatives are also flower visitors.

LIST OF LITERATURE

(1) Beccari, C., and Rock, J. F. A monographic study of the genus Pritchardia. Bishop Museum Memoirs, v. 8: 1921.

(2) Bentham, G. Flora Australiensis.

(3) Brotherus, V. P. Hawaiian Mosses. Bishop Museum, Bulletin 40, 1927.

(4) Brown, Forest B. H. Origin of the Hawaiian flora. Proc. 1st. Pan-Pacific Science Conference. Bishop Museum, Special pub. 7, 1921.

(5) Campbell, D. H. A vacation in the Hawaiian Islands. Bot. Gaz., v. 17, 18, 1892.

(6) ———. On the distribution of the Hepaticae and its significance. New Phytologist, vol. VI, no. 8, 1907.

(7) ———. The new flora of Krakatau. American Naturalist, vol. XLIII, Aug. 1909.

(8) ———. Origin of the Hawaiian flora. Memoirs, Torrey Botanical Club, v. 17: 1918.

(9) ———. The derivation of the flora of Hawaii. Stanford University Publications, 1919.

(10) ———. Some botanical and environmental aspects of Hawaii. Ecology, v. 1, no. 4, 1920.

(11) ———. An Outline of Plant Geography. Macmillan, 1926.

(12) ———. The Australasian element in the Hawaiian flora. American Journal of Botany, Vol. XV, no. 3, 1928.

(13) Chamisso, A. von, and Schlechtendal, D. von. De plantis in expeditione Romanzoffiana observatis. Linnea, v. 1, 1826.

(14) Cheeseman, T. F. Manual of the New Zealand Flora. 2nd Edit. Wellington, N. Z. 1925.

(15) Christensen, Carl. Revised list of Hawaiian Pteridophyta. Bishop Museum, Bul. 25, 1925.

(16) Cockayne, L. New Zealand Plants and their Story. 2nd Edit. Wellington, N. Z. 1919.

(17) Davis, W. M. The depth of coral-reef lagoons. Proc. Nat. Acad. Sci., 9: 1923.

(18) Engler and Prantl. Die natürlichen Pflanzenfamilien.

(19) Ernst, A. The New Flora of the Volcanic Island of Krakatau. Cambridge University Press, 1908.

(20) Forbes, Charles N. Plant invasions on lava. Mid-Pacific Mag., 7: 1914.

(21) Gaudichand, C. Voyage autour du monde. Paris, 1826–30.

(22) Gray, Asa. Botany of the U. S. Exploring Expedition, 1838–1842. Philadelphia, vol. 15, 1853.

(23) ———. Characters of some Compositae in the collections of the U. S. Exploring Expedition. American Academy Proc., v. 5, 1862.

(24) Guppy, H. B. Observations of a Naturalist in the Pacific. London, 1906.

(25) Hillebrand, William. Flora of the Hawaiian Islands. Heidelberg, 1888.

(26) Lyon, H. L. Botany in Hawaii. Bishop Museum, sp. pub. 11, 1926.

(27) McCaughey, V. The phytogeography of Mauoa Valley. Amer. Jour. Botany, v. 4, 1917.

(28) ———. Vegetation of the Hawaiian lava-flows. Bot. Gaz., 64: 1917.

(29) ———. The strand flora of the Hawaiian Archipelago. Bul. Torrey Bot. Club, 45: 1918.

(30) Merrill, E. D. Bibliography of Polynesian Botany. Bishop Museum, Bul. 13: 1924.

(31) Meyrick, E. Macrolepidoptera. Fauna Hawaiensis, 1: 123–275, 1913.

(32) Muir, F. Origin of the Hawaiian Flora and Fauna. Proc. 1st. Pan-Pacific Sci. Conference, Bishop Museum, spec. pub. 7, 1921.

(33) Perkins, R. C. L. Fauna Hawaiensis—Introduction. 1913.

(34) Pilsbry, H. A. Mid-Pacific Land-Snail Faunas. Proc. Nat. Acad. Sci., 2: 1916.

(35) Rock, J. F. The Indigenous Trees of the Hawaiian Islands. Honolulu, 1913.

(36) ———. A monographic study of the Hawaiian species of the tribe Lobelioideae, family Campanulaceae. Bishop Museum Memoirs, v. 7: no. 2, 1919.

(37) Skottsberg, Carl. Juan Fernandez and Hawaii. Bishop Museum, Bul. 16: 1925.

(38) Stephani, F. Index Hepaticarum. Bull. de l' Herbier Boissier, 1898–1908.

(39) Stevens, F. L. Hawaiian Fungi. Bishop Museum, Bul. 19, 1925.

(40) Treub, M. Notices sur la nouvelle flore de Krakatau. Ann. du Jardin Botanique de Buitenzorg, 7: 1888.

(41) Wallace, A. R. Geographical Distribution of Animals. 2: 277–278.

ON THE SURVIVAL OF SPERMATOZOA IN THE FEMALE GENITAL TRACT OF THE BAT

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IT IS the current view that autumn constitutes the mating season of bats but that ovulation and fertilization are deferred until spring. By implication, the spermatozoa survive hibernation in the uterus (*Vespertilionidae*) or in the vagina (*Rhinolophidae*) where indeed they may be found at any time during the winter. This view Mr. W. Kenneth Cuyler and I have questioned (1927) on the basis of some years of observation on several species of Texas bats, studies which Mr. Cuyler expects some time to carry to a conclusion, as much material is already in hand. In the meantime, however, in connection with other studies on the mammalian reproductive cycle, the problem of the length of life of spermatozoa in general has forced itself upon my attention. I have, therefore, been over the entire literature again, which seemed all the more profitable in view of the publication of some important papers in recent years, notably those of Courrier, Nakano, and Redenz. Inasmuch as the significant literature is scattered and is without exception French or German, it seems worth while to review the topic for the benefit of others interested in the subject.

The problem began with Pagenstecher (1859) who found that on a certain January 23 the bat uterus was filled with sperms (*Vesperugo pipistrellus*), and that ovulation had not yet taken place. Van Beneden, however, finding spermatozoa about the ovaries and dividing tubal ova in December, January, and February, concluded that ovulation took place in the fall but that the ovum was arrested in its development, lying dormant until spring, a situation comparable to the arrest of development which Bischoff first described for the deer, Fries for the badger, and Patterson for the armadillo. It may be stated in passing that van Beneden has always stood alone in his interpretation. He was doubtless misled because he brought his subjects into the warm room, thus artificially ending their hibernation and speeding up the developmental process.

Three further authors (Benecke, Fries, and Eimer) published short but interesting papers in the second volume of the *Zoologischer Anzeiger* (1879). Benecke had access to several hundred specimens of *V. pipistrellus* and *Plecotus auritus* throughout the winter and uniformly found the uterus filled with a creamy mass containing active spermatozoa. The uterine tubes contained no sperms before spring. As early as December in one ovary or the other he found a graafian follicle already well enlarged, a point corroborated and emphasized by Courrier 50 years later. Benecke states that this follicle could be made to enlarge still more by keeping the bats in a warm place and feeding them; but he gives no details of such experiments. In the spring some sperms are said to travel up the oviduct; and the author makes the remarkable statement that he actually saw them through the thin wall of the tube. After fertilization the sperm mass is expelled.

Fries studied specimens of nearly a dozen species and clearly stated the case for the fall mating and the winter storage of spermatozoa. He recorded the new observation that the *Rhinolophidae* are exceptional in that in this family the female stores the sperm mass in the greatly distended vagina. He also studied the males and found their genital tracts swarming with live sperms and the accessory glands in a highly active state. The young born in the spring, he stated, are not mated in the fall but wait over until the following spring (*Vespertilio murinus*).

Eimer made a preliminary report in 1878, a more extended study (1879) after Fries's paper appeared. He kept individuals of *Vesperugo noctula* throughout the winter, examining the females from time to time and always with the same result: sperms in the uterus. The experiment was an excellent one and should be repeated and extended, as will be explained below, because Eimer failed to report the crucial point, namely, whether or not he kept males and females together.

These three authors were soon corroborated in all essential details by Vogt and by Robin in 1881. Robin stated that new copulations may take place on warm days of winter or during the early days of spring, a conclusion based upon actual observations on the horse-shoe bat (*R. ferrum-equinum*). Vogt thought that the tardy copulations of spring (horse-shoe and murine bats) concerned the virgin yearlings, for at this time one finds three kinds of individuals: (1) virgins with small graafian follicles and no sperms in the uterus; (2) females with uteri distended by a mass of sperms, mucosa edematous or seen detached in places; (3) females already ovulated. He agreed with Robin that the male remains fertile throughout winter for these supplementary matings.

Of the work thus far reviewed the embryologist Duval (1895) gave a rather complete account. He concluded that the adult females copulate but once a year, namely, in the fall, but the young females of the season wait over until spring and are impregnated then. Disagreements as to exact time of ovulation, gestation, and parturition he attributes to species differences. Duval observed three copulations on May 25, 1893, and gives a description of the act (p. 107). He also quotes Jobert (1872) who described parturition in the bat, which has been observed but two other times, namely, by Rollinat and Trouessart (1896) and by Sherman (1930).

That bats may also copulate in the spring was further asserted by Salvi (1902) and by van der Stricht (1909), although both base this conclusion upon their finding empty uteri in a small percentage of females in the early spring.

THE WORK OF ROLLINAT AND TROUESSART

In 1895 Rollinat and Trouessart also published two papers on the subject, covering collections made December 7 to January 15. These were preliminary to their extensive studies of 1896 and 1897, and confirmed the previous work and added several new points of interest. They discovered in the male a "bouchon urethral" or hard plug moulded to the wall of the urethra and persisting throughout hibernation. They presume the plug to consist of secretions from the accessory reproductive glands, especially the urethral gland of Robin (1881). Since in the *Rhinolophidae* the vagina is filled with the vaginal plug consisting of spermatozoa imbedded in firmly coagulated secretions of the male glands, Rollinat and Trouessart think that copulations during the winter are hardly possible, though Courrier (1924) suggests that the male with his os penis is quite capable of penetrating the vaginal plug. Rollinat and Trouessart marvel at

the astonishingly high degree of activity of the male glands throughout hibernation, which is such that the true rutting season would seem to be spring, as it is for most European mammals. In these preliminary papers the authors still interpret the continued activity of the male organs to serve the useful purpose of impregnating in the spring young virgin females born the preceding season. Like all their predecessors, Rollinat and Trouessart labor under the impression that spermatogenesis likewise continues in winter, a mistake only lately corrected by Courrier (1924) and by Nakano (1928).

In both their later papers (1896 on *V. murinus*, 1897 on *R. ferrum-equinum*) Rollinat and Trouessart, however, deny all matings for bats in winter or spring, holding, in other words, that the only rutting season is that of autumn. Contrary to their former opinion, therefore, they state positively that the virgin females born in June or July wait over until the fall of the succeeding year. They thus reverse their former opinion despite the fact that they, as well as others, actually witnessed copulation in the winter. They state, however, that a given female may copulate repeatedly in the fall, as evidenced by the increase in the size of the sperm mass as the season advances. The mass finally reaches a size much greater than any male could supply at a single ejaculation. The authors further postulate a sort of "Brown-Sequard" effect upon the male soma due to the resorption of sperms from the genital tract.

An interesting observation by these French workers concerns the leakage of spermatozoa into the bladder, whence they are evacuated with the urine, an observation which Nakano (1928) mistakenly believed he was the first to make. Rollinat and Trouessart significantly observed also that the bat population in caves, walls and belfries is not stationary but shifting. On warm evenings bats (especially *V. pipistrellus*) may frequently be seen flying about in the open. Males and females usually are found occupying separate quarters.

The authors describe a copulation and, in considerable detail, a parturition.

THE WORK OF GROSSER

The next study to be mentioned is a short one by Grosser (1903) recording what he calls a connective tissue atresia of the vagina. This seems a rather misleading title. What happens is that after copulation, which in *V. noctula* occurs soon after parturition in July, the proximal portion of the vagina not only undergoes the usual tremendous cornification of the vaginal epithelium, completely plugging the canal, but it also becomes denuded of epithelium because this sloughs off from the subjacent connective tissue. The plug remains as a cord in the vagina until expelled in the spring, when regeneration of the epithelium takes place. Assuming that further copulation is impossible to females in this condition, Grosser feels that his observation offers the best proof of the long survival of sperms for the eight months that the "atresia" lasts. It is quite clear, however, that what Grosser described agrees with Courrier's extensive findings, now to be mentioned, although Grosser is the only one yet to describe the complete denudation of the cornified layer in a given region of the vagina.

Grosser's short paper remained the single study undertaken on the sexual cycle of the bat by modern histological methods, although the broad facts had become common property by 1900. In 1895, however, Duval still complained that these facts had not yet become incorporated in the zoological textbooks of the day. It remained for Courrier (1924, 1927), student of Bouin, to work up the problems from the modern

viewpoint. Nakano (1928) published a histological study without being aware of either Courrier's work or those of Rollinat and Trouessart. Finally Redenz (1929) submitted the store of spermatozoa to experimental study with illuminating results.

THE WORK OF COURRIER

Courrier's two thorough studies go a long way towards establishing the prevailing idea of the long life of bat spermatozoa. He made excellent preparations of both female (1924) and male (1927) genitalia of a variety of bats, the most complete series being those of *V. pipistrellus*, *Miniopterus Schreibersii* and *V. serotinus*.

Among these *M. Schreibersii* was found to be exceptional for bats in that in this species copulation, ovulation, and fertilization occur in the fall, pregnancy ensuing at once and continuing during the winter. The male reproductive organs, the accessory glands as well as testes, undergo involution and remain in the "resting" stage or anoestrum until the next breeding season a year later. Neither the male nor the female retains a store of spermatozoa and the species thus conforms to other mammals having a single limited breeding season annually.

V. pipistrellus, on the other hand, is typical of bats. Its story is as follows: The summer months witness a regeneration of the spermatogenic tubules of the testes. After parturition and lactation copulation takes place and throughout winter the uteri remain filled with mucous masses laden with highly active spermatozoa. Courrier for the first time showed that the spermatogenic function rapidly ceases, a fact overlooked by Rollinat and Trouessart and their predecessors. The testes shrink, as does also later the head and body of the epididymis, while its tail hypertrophies greatly and harbors myriads of highly motile spermatozoa. The "follicular phase," however, continues in the female; and from the beginning of winter on one may recognize the follicle destined to rupture in the spring. As a result of this long continued follicular secretion, the vaginal mucosa proliferates until the lumen becomes completely obliterated by a veritable "bouchon vaginal," which is not, however, homologous with the vaginal plug that results from copulation in rodents and other forms, but consists, in the bat, entirely of epithelial cells from the vaginal wall, as first noted by Grosser (1903).

In the condition just described the males and females remain throughout winter. In the spring the plug is cast out and ovulation, fertilization, and pregnancy result.

In the *Rhinolophidae* the spermatozoa are retained, not in the uterus, but in a pocket on the ventral surface of the vagina at a point already indicated by a thin area in the epithelium in young virgin females.

In both the *Vespertilionidae* and the *Rhinolophidae* the accessory male reproductive organs remain highly active throughout winter, despite the degeneration of the spermatogenic tubules of the testes, while the interstitial tissue remains well developed. Hence the latter is made responsible for the endocrines which condition these secondary sex organs.

THE WORK OF NAKANO

From the work of Nakano (1928), who was investigating the glycogen of the genital tract, we learn that the Japanese *Vespertilio abramus* follows the same cyclic changes of the *Vespertilionidae* of Europe. He noted the reservoir of sperms in the cauda epididymidis of the male and in the uterus of the female. Glycogen appears in the uterine epithelium as well as in the tail of the epididymis shortly after sperms arrive in these organs. Glycogen in the

uterus is interpreted as of nutritive value to the spermatozoa, which may be correct if it can be shown that spermatozoa are ever capable of absorbing nutriment at all (*v.i.*). Nakano made the very significant discovery that the spermatozoa of the uterus were non-motile so long as they remained within the matrix in which they are imbedded. The observation was followed up by Redenz (1929) who contributed an illuminating experimental study.

THE WORK OF REDENZ

Redenz submitted fourteen females to examination. Two *Plecotus auritus* females were taken March 5 and 18 respectively while still in the torpor of hibernation. The former was the only female of the collection in which sperms were recovered from the uterine tubes. A mass of sperms was found in each of these two uteri. In most of the other specimens, which belonged to the species *V. murinus* and were captured April 11, 18, and 25, ova were found free in either the tube or the uterus. Sperms were recovered from the uterus in only two of these cases, the sperm masses having been expelled in all others. Most of the specimens, therefore, added little to the problem in hand; but the author presents for the first time some excellent photomicrographs of bat tubes containing ova in cleavage. The author's contribution to the physiology of the spermatozoa is more significant.

In going over the literature reviewed above one notes that former investigators uniformly reported the spermatozoa stored in the bat uterus in winter to be in a very active state. The reviewer has examined dozens of bats of several species by the same faulty technique and with the same result. Nakano (1928) and Redenz (1929) now find that the motility thus observed was due to the dilution of the sperm mass with the salt solution in which the specimens were examined. Without dilution the sperms are seen to remain absolutely motionless. If a fragment of the sperm mass is placed in Ringer's solution one may observe that the spermatozoa at the surface become more and more motile and gradually swim away; then those in deeper layers follow. At room temperature the motility lasts 16–20 hours, at the end of which time the sperms die. It is the function of the matrix containing the sperms to inhibit the motion so as to prolong their life.

In spring, then, according to the picture drawn by Redenz, ovulation occurs, the follicular fluid and other secretions descend into the uterus, and under their diluting or dissolving influence, "platoon after platoon of sperms" are "detailed off" to ascend the tube and seek the ovum awaiting their arrival.

FACTORS FAVORING THE SURVIVAL OF SPERMATOZOA

Such are the facts concerning the reproductive habits of bats so far as they have been ascertained to date. Are they sufficient to warrant the statement that the bat sperms survive in the female genital tract for from five to eight months? What is the answer in the light of comparative studies and in the absence of the direct experimental proof?

The first general condition favorable to the survival of the spermatozoa in the bat is its low body temperature. The animal is practically poikilothermous. Courrier found the mouth temperature to be 4° to 10°C., Redenz 14°. The latter is pretty near the temperature at which mammalian spermatozoa will live the longest in salt solution in vitro (cf. Hartman, 1932). Courrier found the rate of involution of the accessory sex glands of the male after castration to be extremely slow in winter, as also the rate of Wallerian degeneration

in several nerve tracts. Aron (1923) found similarly that castrated Tritons lost their secondary sex characters much more slowly in the cold than in the warm. In contrast to the condition in guinea pigs, in which, after castration, the spermatozoa of the epididymis die in 16 days, in bats they live for 60 days after castration (Courrier).

Parallel cases are to be found in fishes and Amphibia. Thus van Oordt (1928) states that the well known aquarium fish *Xiphophorus Helleri* may bring forth seven broods over a period of 10 months after a single mating. *Salamandra maculata* gives birth to young in May, whereupon a new batch of eggs are said to be fertilized from sperms stored in July (Gadow). There are also numerous cases in the invertebrates, as e.g. in the highly organized *Octopus vulgaris*, which, as Belonoschkin (1930) found, copulates from May to August. In the upper (secretory) third of the oviduct he found a sperm mass (non-motile until diluted) in which the sperms are said to survive until the following spring.

The second factor favorable to the longevity of the ripe spermatozoa is their immobility brought about by the medium in which they are placed. This immobility in the bat, discovered by Nakano and confirmed by Redenz, is, however, but illustrative of the general law that spermatozoa are endowed with a limited supply of energy and when this is used up they die. Wherever spermatozoa are stored there is a provision for the inhibition of their movement. They are motionless in the testis of the sea-urchin but when dispersed in sea water they become instantly highly motile. Sperms are inhibited in the mammalian testes but when ejaculated become motile and in the female genital tract are short-lived because of their high degree of activity. It is improbable that ripe spermatozoa are capable of absorbing any nutriment from the surrounding medium.

A further pursuance of this question is, however, out of place here. The reader is referred to the chapter on "Mass Physiology of Spermatozoa" in Allee's *Animal Aggregations*, 1931.

DO BATS COPULATE IN SPRING?

The facts thus far reviewed point to the reasonableness of the current interpretation of the breeding habit of most bats, namely, that the spermatozoa which the female receives in one or several matings in the fall (August to October according to species) live until spring and are the identical ones which function in fertilization at the end of this period. Yet it must be remembered that the conclusion is entirely inferential, for no one has yet, as already indicated, kept isolated females from fall to spring and seen them pregnant at the end of the hibernation. Eimer's experiment in this direction is incomplete in several respects. The alternative theory, namely, that bats copulate during warm spells in winter and again in the spring just before the time to ovulate, has arguments in its favor. Robin, Vogt, Duval, and Rollinat indeed, witnessed matings in these seasons and van Beneden secured eggs in cleavage from bats in the winter months. It is, therefore, certain that just as soon as female bats are subjected to warmth they are ready to copulate and, given sufficient time, to ovulate and conceive. As to the segregation of the sexes during hibernation, which seems to be the rule, Rollinat and Trouessart speak of the bat populations of crevices and caves shifting their position from time to time throughout winter and in mild weather fluttering out in the open. It should also be pointed out that in those species that mate in July and August, the store of spermatozoa may be subjected to elevated temperatures which sometimes

prevail in September before the winter sleep comes over the animals.

Whatever view one is inclined to accept on the present problem the temptation is great to become teleological and ask: if autumn marks the real mating period, why the colossal storage of sperms in the tail of the epididymis and why the continued hypertrophy of the accessory sex glands of the male? The most likely answer one can make is that, contrary to the opinion of Rollinat and Trouessart, the males are still in a condition to impregnate the young females of the previous year. It seems rather wasteful, however, that all the males should reserve their potency and fertility for the benefit of the debutantes of spring not yet mature at the last harvest season.

The chief consideration, however, that leads to a questioning of the current interpretation of the bat cycle is the fact that in those species in which the male is free of sperms in winter the female is likewise free of sperms. The case of *Miniopterus Schreibersii* has already been noted. In this species copulation, ovulation, fertilization are closely connected events. The male performs his procreative function, whereupon his organs atrophy until the next year. A similar case is that of *Nyctinomus mexicanus* of Texas, whose breeding season Mr. Cuyler and the reviewer found to occur only in spring. There is the same opportunity for mating as in other species of the same locality that do mate; but in *Nyctinomus* the organs of both sexes are in the resting stage in which they remain until spring. Perhaps these cases are the more primitive, conforming as they do to the habits of mammals in general; the more typical cheiropteran behavior might, therefore, be thought of as developing secondarily. The latter is peculiar in several other respects. Whereas in rodents mating ensues immediately after parturition, in bats it follows weaning of the young. Mating moreover occurs in the absence of ripe follicles. In other respects bats are still to be brought into the picture of what we conceive to be typically mammalian reproductive behavior.

SUMMARY

Typically, bats mate in autumn after the female has weaned her young, at which time the post partum involution of her organs is complete and a new sexual cycle may be said to have begun. In the male spermatogenesis has passed its zenith and the testis has begun involuting; but the epididymis, especially the tail, is greatly distended with sperms, while the accessory glands (prostate, seminal vesicle, urethral gland of Robin) are enlarged and highly secretory. This condition is maintained with greater or less diminution until spring. Involution of the male organs occurs while the female is pregnant but regeneration follows promptly in summer. Oestrus in the female (follicular phase) continues from fall until spring or six to eight months; hence pregnancy and lactation alone interrupt her oestrus and she may be said to have no anoestrum. The male has but a short anoestrum (March to July), for his sexual vigor and fertilizing capacity is maintained by interstitial tissue (Courrier) from July to March, even though during the larger portion of this time spermatogenesis is in abeyance.

Two exceptions to this rule are known: (1) *Miniopterus* which breeds only in fall; here anoestrum lasts in the male from October to July (Courrier); (2) *Nyctinomus*, which breeds in the spring and here anoestrum lasts from May to March (Cuyler and Hartman). The California mastiff bat may also belong to this class (Howell, 1920). Since this represents the ordinary mammalian condition it probably consti-

tutes a remnant of the primitive cheiropteran condition.

The mass of spermatozoa typically found in the female genital tract at any time in the winter is, according to the current view, supposed to survive hibernation (6–8 months) and remains available for fertilization in the spring. For such survival the lowered body temperature of the poikilothermous bat (10°–14°C.) and the mechanism for immobilization of the sperm in a coagulum constitute extremely favorable conditions. Nevertheless it is the purpose of this paper to point out that the proof has not yet been forthcoming finally to establish the view that the sperms ejaculated in the fall are the ones that will fertilize the ovum in the spring. Observed winter and spring copulations speak in favor of repeated copulations in these seasons. The crucial experiment, which is quite feasible and has already been partly carried out by Eimer, consists of capturing females in the fall, keeping them isolated from males throughout winter and observing whether or not a pregnancy ensues at the end of hibernation.

Regardless, however, of the outcome of such an experiment on the female, the long life of spermatozoa in the epididymis of the male is undoubted, for both Courrier and Nakano have demonstrated the cessation of spermatogenesis as long as seven months prior to the final disappearance of the last summer's crop of spermatozoa from the tail of the epididymis.

LIST OF LITERATURE

Aron, M. 1923. Influence de la température sur l'action de l'hormone testiculaire. C. R. Acad. Sci., 178: 141.

Benecke, B. 1879. Ueber Reifung und Befruchtung des Eies bei den Fledermäusen. Zool. Anz., 2: 304.

Belonoschkin, B. 1929. Das Verhalten der Spermatozoen zwischen Begattung und Befruchtung bei Octopus vulgaris. Zeitschr. f. Zellforsch., 9: 750–753.

Courrier, R. 1927. Étude sur la déterminisme des caractères sexuels secondaires chez quelques mammifères à activité testiculaire périodique. Arch. de Biol., 37: 173–334.

Duval, M. 1895. Sur l'accouplement des chauves-souris. C. R. Soc. Biol., (Feb. 23), 47: 135–136.

———. 1895. Études sur l'embryologie des Cheiroptères. Première partie. Jour. de l'Anat., et de la Physiol., T. 31, 93 pp.

Eimer. 1879. Ueber die Fortpflanzung der Fledermäuse. Zool. Anz., 2: 425.

Fatio, V. 1869. Faune des Vertebrés de la Suisse. Mammifères. (p. 23, copulation of bats.)

Fries, S. 1879. Ueber die Fortpflanzung der einheimischen Chiropteren. Zool. Anz., 2: 355. Also Göttinger Nachrichten. No. 11, 1879.

Grosser, O. 1903. Die physiologische bindegewebige Atresie des Genitalkanales von Vesperugo noctula nach erfolgter Kohabitation. Verhandl. d. anat. Gesellschaft, Heidelberg, Anat. Anz., Ergänzhft., 23: 129–132.

Hartman, Carl G. 1932. Ovulation and the transport and viability of the ovum and sperm in the female genital tract. In Edgar Allen's "Sex and Internal Secretions," Williams and Wilkins, Baltimore.

Hartman, Carl G., and W. Kenneth Cuyler. 1927. Is the supposed long life of the bat spermatozoa fact or fable? (Abst.) Anat. Rec., 35: 39.

Howell, A. Brasier. 1920. Contribution to the life history of the California Mastiff bat. Jour. Mam., 1: 111–117.

Leydig. 1850. Zur Anatomie der männlichen Geschlechtsorgane und Analdrüsen der Säugethiere. Ztschr. f. Zool., V. 2.

Nakano, O. 1928. Ueber die Verteilung des Glykogens bei den zyklischen Veränderungen in den Geschlechtsorganen der Fledermaus und über die Nahrungsaufnahme der Spermien in den weiblichen Geschlechtswegen. Folia anat. Japon., 6: 777–828.

Pagenstecher. 1859. Uebei die Begattung der Vesperugo pipistrellus. Verhandl. d. naturhist.-med. Verein zu Heidelberg.

Redenz, E. 1929. Das Verhalten der Säugetierspermatozoen zwischen Begattung und Befruchtung. Zeitschr. f. Zellforsch., 9: 734–749.

ROBIN, A. 1881. Sur l'époque de l'accouplement des Chauves-souris. Bull. Soc. philomat., 7e Ser., 4: 88.

ROBIN, H.-A. 1881. Recherches anatomiques sur les mammifères de l'ordre des Chiroptères. Thèse. Fac. des Sci., Paris. Also: Ann. des Sci. nat.; Zool., Art. 2, 12: 117.

ROLLINAT, R., and E. TROUESSART. 1895. Sur la reproduction des Cheiroptères. C. R. Soc. Biol., Jan. 26, 47: 53–54.

———. 1895. Deuxième note sur la reproduction des Chiroptères. *Ibid.*, July 6.

———. 1895. Sur la reproduction des Chauves-souris. Bull. Soc. Zool. France, Proc. Session Jan. 22; 20: 25–28.

———. 1896. Sur la reproduction des Chauves-souris. Vespertilio murinus. Mém. Soc. Zool. France, 9: 214–240.

———. 1897. Sur la reproduction des Chauves-souris. Les Rhinolophes. *Ibid.*, 10: 114–138.

SALVI, G. 1901. Observations sur l'accouplement des Chiroptères de nos pays. Processi verbali della Soc. Toscana di Sci. Nat. Review in Arch. Ital. de Biol., 1902, 37: 474.

SHERMAN, H. B. 1930. Birth of the young of Myotis austroriparius. Jour. Mamm., 11: 495–503.

VAN BENEDEN, E. 1870. Recherches sur la composition de l'œuf, etc. Mém. de l'Acad. royale des Sci., des Lettres et des Beaux-arts de Belgique. Vol. 34, 285 pp., 1867–1870.

———. 1875. La maturation de l'œuf, la fécondation et les premières phases du développement d'après les recherches faites sur la lapin. *Ibid.*, 40: 686–736,

VAN BENEDEN, E., and CHAS. JULIN. 1880. Observations sur la maturation, la fécondation et la segmentation de l'œuf chez Cheiroptères. Arch. de Biol., 1: 551–571.

VAN DER STRICHT, O. 1909. La structure de l'œuf des mammifères (Chauve-souris, Vesperugo noctula) 3e Partie. Mém. de Sci. de l'Acad. roy. de Belgique. Ser. 2, T.2.

VOGT, CARL. Assoc. franc. pour l'avancement des Sci. 10e session, C. R. p. 655. (Corroborates Benecke and Eimer.)

SEX PROBLEMS IN HEMP

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ALTHOUGH sex has been recognized in animals since before the time of recorded history the recognition of sex in plants is, with few exceptions, less than 250 years old. In Mesopotamia and in Egypt, where the date palm has been cultivated for ages, the distinction of male and female palms has been made for at least 4000 years as shown by inscriptions describing and illustrating the manner of pollinating the female flower clusters by racemes of male blossoms, in practically the same way as that still used by the Arabs and Egyptians. The earlier herbalists ascribed sex to various plants. Thus one kind of fern was called Male Fern and another Female or Lady Fern, and one kind of Dogwood was named *Cornus mas* and another *C. foemina*. These differences, however, were specific or even generic and had nothing to do with the sex of the plants.

The failure to distinguish sex in plants is due to the fact that in the popular mind sex distinction is associated with distinction of *individuals* of different sex, as in the domestic animals and in man. In Europe hemp and the hop were the only commonly cultivated plants in which the plants are dioecious. Here the pollination is accomplished by air currents and there is nothing similar to the sexual processes in animals. The remainder of the commonly cultivated plants possessed perfect flowers and in some of them, wheat, barley, oats, pea and bean, are usually pollenized *before* the flower had opened. Thus the necessity for sex was not recognized.

Nehemiah Grew in 1682 indicated the stamens as male organs and the pistils as female organs, from morphological reasons only. Camerarius in 1694 was the first investigator to report the results of actual experiments by which he proved the correctness of Grew's assumptions. He excluded pollen from the pistils of *Mercurialis*, *Morus*, *Zea mays* and other plants and obtained no seeds except when he applied pollen from the male flower of the same species. The publication of the results of these experiments was followed by numerous experiments both in Europe and in America which confirmed the sexual nature of stamens and pistils and led soon to successful attempts at hybridizing various kinds of plants.

Hemp, *Cannabis sativa*, is a native of Asia and has been cultivated both for its fibre and for the drug "hashish" which is in great demand in Central Asia, Persia, Afghanistan and Northwestern India. Its culture as a fibre plant has spread all over the temperate regions of the world and it has escaped and become a weed of low lands in various places. Thus it is very abundant along the Missouri River and tributary streams in Eastern Nebraska and Western Iowa.

The plant as grown for fibre is 8 to 12 feet or more tall while the varieties grown for the drug are usually only about 3 to 4 feet tall. The male plants are usually more slender than the female plants, sometimes slightly paler green, and have but few and small leaves at the top. The clusters of male flowers are large and conspicuous. As soon as the pollen has all been

shed the plants die, long before the female plants. The latter are usually stouter and leafy to the apex, the flower clusters being smaller and less conspicuous (before the seeds begin to form). The female plants have a strong, somewhat pungent odor, especially after the seeds are beginning to form.

Normally, when sown in the summer time, about 45 to 47 per cent of the plants that grow to maturity will be males, but the ratio may vary considerably in adjacent plats from the same lot of seed. Sometimes up to 55 per cent will be males. Usually the male plants will have no female flowers but a small percentage of the female plants will develop, as they grow older, a few male flowers. In 1926 or 1927 the writer found a plant, resembling a male plant in habit, with perfect flowers, the pistil and stamens apparently being functional. The flowers did not develop until just before an early frost which destroyed the plant.

THE EFFECT OF AGE OF POLLEN

Perhaps the first systematic experiments to determine the factors involved in the determination of sex in any plant were those begun by Dr. Theophilus Ciesielski in 1871 in Poland. These experiments covered a series of eight or ten years or possibly longer, but were not reported until 1911. The earlier experiments had to do with the effect of close or distant planting, with only negative results. Planting at different phases of the moon also was without effect upon the sex ratio. Growing the plants in light and in shade, in moist and in dry soil, and in rich and in poor soil were also equally ineffective. The ratio remained about the same; 40 to 50 per cent of the plants were males, the remainder females. Similar result were obtained whether the pollen was taken from the top, middle or lower portion of the inflorescence. The only definite results were those where the pollen used was of different ages.

In the male hemp plant the stamens usually begin to dehisce a little while after sunrise when the atmosphere begins to become drier. These flowers were collected early in the morning shortly before the stamens opened and the pollen from some of these was scattered on the flowers of female plants placed indoors or at a considerable distance to prevent chance pollination. Some of the male flowers collected at sunrise were kept until sunset and were then used to pollenize other female flowers. With slight variations as to details these experiments were repeated several years. The seeds were saved and planted out-of-doors next summer. From the flowers pollenized with freshly produced pollen the seeds gave 85 to 90 per cent male plants while the seeds from flowers pollinated with 12 hour old pollen gave 90 to 100 per cent female plants. Ciesielski emphasizes the fact that he repeated these experiments several successive years, always with the same results. He concludes, therefore, that there is a tendency toward maleness in fresh pollen and that as the pollen becomes old this tendency changes from maleness to femaleness.

In 1921 Lilienfeld reported the results of experiments performed by him to test the correctness of Ciesielski's conclusions. He could not find any differences in the sex ratio whether the pollen used was fresh or 12, 30 or 36 hours old.

Ignorant of Lilienfeld's work the writer began experiments along the same line a short time later. This work was carried out in the greenhouse at first and then out of doors. The number of seeds obtained in the greenhouse experiments was too small to enable any definite conclusions to be drawn. Out of doors the female inflor-

escences were bagged and allowed to remain covered one or two weeks. Then the bags were temporarily removed and all flowers whose ovaries had started to enlarge (indicating pollination before bagging) were removed. Then the flowers were pollenized with pollen of the desired age and again covered until the male plants were all removed a few days later. Pollination was accomplished in various ways. For fresh pollen in most cases anthers were selected that were just opening and the pollen dusted from these on the female flowers. Sometimes unopened anthers were torn open and the contents applied to the stigma. The flowers were then rebagged. For older pollen, clusters of male flowers on the point of opening were bagged early in the morning after removal of all previously opened flowers. Since nearly all of the male flowers open at about the same time the pollen in the bag will be approximately of equal age when the bag is removed from the inflorescence. Such bags of pollen were held various lengths of time. When it was desired to use pollen of any given age the corresponding bag of pollen was placed on a female influorescence that had been bagged as described above, and shaken and beaten until all the flowers were pollinated. This bag was allowed to remain or a fresh bag was placed over the inflorescence until all bags were removed after the destruction of all male plants. Pollen used in these series of experiments was fresh, 8–9 hour, 14–16 hour, 24 hour, 42 hour and 64 hour pollen.

The seeds resulting from these pollinations were planted next year and the ratios of male and female plants determined when they began flowering. The plants grown in 1926 from pollinations made in 1925 gave for "fresh" pollen 44.2 per cent male plants, the control from open pollinated seeds from other branches of the same parent plants giving 49.3 per cent males. The seeds produced from "old" pollen gave 43.4 per cent male plants and their controls 48.7 per cent males. In 1927 the figures for seeds resulting from 1926 pollinations were 47.2 per cent males for "fresh" pollen, 53.5 per cent males for 10 to 12 hour old pollen, and 47.1 per cent males from pollen 17–27 hours old. The controls were respectively 53.5 per cent, 49.9 per cent and 50 per cent males. Although the figures showed considerable variations it is clear that they agree rather closely with those obtained by Lilienfeld and do not give any support to Ciesielski's reports. Either the latter failed to make accurate experiments or the variety of hemp used by him responded in an entirely different manner from the varieties used by Lilienfeld or the writer.

THE EFFECT OF MUTILATION

The sex question in hemp had already been attacked from another angle by Pritchard in the years 1909–1914. This investigator removed the flowers and flower buds and even leaves and portions of the tops from various hemp plants of both sexes. Omitting the earlier experiments in which the numbers involved were few the results of his 1913 mutilations may be considered. Fourteen male plants which bore no female flowers had all their flowers and flower buds removed. Eleven of these produced only male flowers on their new growth but on two of the plants a few sex-intergrade flowers and female flowers appeared among the male flowers (four female flowers to 7390 male flowers) and one produced all (461) female or intersex flowers. Of the 31 female plants that had their flowers removed four had at the time a few male blossoms, a total of 1016 male to 29,950 female flowers, or a little over 3 per cent. After new growth took place these four plants gave 17,137 male

blossoms and 18,861 female blossoms, or almost 48 per cent male plants. The twenty-seven female plants that had no male blossoms at first had on their new growth 160,862 flowers of which 24,242 were male (or intersex) flowers, approximately 15 per cent.

In connection with the foregoing effects of mutilation upon the sex ratio in hemp may be noted the report of J. E. Higgins upon *Carica papaya*, in which sex changes have been brought about in a similar manner. This herbaceous tree, if it may so be called, is normally dioecious although trees with hermaphroditic flowers are not rare. Upon cutting back a male tree it frequently happens that the new shoots produce female flowers or hermaphroditic flowers, but Higgins could not induce female trees to change their sex by cutting them back.

SEX CHROMOSOMES

The discovery of chromosome differences in the two sexes of certain insects thirty years ago, followed by the realization that this is a very general condition throughout most of the animal groups, led to investigations to determine whether similar conditions held in those plants in which the sexes are separate. The earlier studies by Strasburger gave negative results but in 1917 C. E. Allen reported sex chromosomes in *Sphaerocarpus*, one of the Hepaticae. Six years later they were reported in a number of Dicotyledons and in one Monocotyledon. Among the former was the hop (*Humulus lupulus*), a near relative of hemp. In the next year, 1924, Hirata, a Japanese investigator, found both X and Y chromosomes in one variety of hemp. The male plants were heterozygous with 18 autosomes + X + Y and the female plants homozygous, 18 + X + X. The male gametes were of two kinds, with either X or Y chromosomes + 9 autosomes. The female gametes all had 9 autosomes + X. In another variety the two could not be distinguished by size and shape. McPhee in the same year reported his investigations in which the variety of hemp studied did not show distinguishable differences between X and Y chromosomes.

THE EFFECT OF LIGHT

In the meantime Dr. J. H. Schaffner had been carrying on studies on the sexual expression in hemp and other dioecious and monoecious plants. Planting hemp seeds in December he obtained approximately equal numbers of plants that had the aspects respectively of male and female plants. However, 88 per cent of the female plants produced some intersex flowers or some purely male flowers and 84 per cent of the male plants produced some intersex flowers or female flowers. These plants were the descendents from two generations of plants that when grown in the summer were pure male or female with no intersexes. Only a few of the flowers showed complete sex reversal, most of them being intermediate, with malformed and nonfunctional stamens and pistils or organs showing the characters of both, e.g. stamens bearing stigmas, or pistils with microsporangia. The few complete reversals consisted of normal male flowers producing functional pollen on the female plants and, much more rarely, normal female flowers on male plants. This author is very emphatic in his conclusions that the sexual differentiation is not explicable by a "Mendelian hypothesis of sex" but is the result of environmental factors. The particular factor involved in the experiments just described was the "abnormal environment, mainly a lack of light." The author carried out further experiments which led him to conclude that not merely shortened daylight but also reduced fertility

of the soil increased the tendency toward sex-intermediacy or sex reversal.

McPhee repeated some of these experiments with several different strains of hemp, using chambers which could be closed at different times of day so that the plants could all be grown during the summer and yet have different daylight periods. Although he did not obtain such striking percentages of change as Dr. Schaffner did he found that with the shortening of the daylight the percentage of intersex flowers was increased, although the plants retained their general aspect of male or female plants. He was successful in obtaining a few viable seeds from female flowers produced on male plants and pollenized by pollen from the same plants. Only four such seeds produced plants that grew to flowering. Of these three were male plants and one female. On the other hand many more seeds were obtained from flowers on female plants pollenized by pollen from male flowers on the same plant. Out of 161 such plants grown to flowering, 158 were typical female plants. The three male plants are believed by McPhee to have been due to accidental pollination from male plants. Flowers on these female plants were pollinated from male flowers produced on the same plants under the influence of shortened daylight and from these a few second generation plants were obtained, like their parents all female. Apparently the condition of femaleness is a matter of heredity.

McPhee found that there was great difference in the ability of various strains of hemp to be affected in the sex ratio by different lengths of daylight. Some strains appeared to be entirely unaffected by such treatment and produced pure males or pure females, regardless of the shortening of the daylight period. Other strains were very readily modified by the same treatment.

DISCUSSION

When we bring together the various observations with reference to the sexual conditions in hemp we find a number of apparently contradictory conditions. In at least one variety of hemp Hirata has demonstrated the presence of distinguishable X and Y chromosomes, the male plant being heterozygous and the female homozygous. In other varieties these chromosomes are not distinguishable but it can hardly be doubted that they are there even though alike in appearance. The plants grown from seed whether in summer daylight length or in shortened light periods are in about equal numbers, male and female, so far as the vegetative characters are concerned. Yet by cutting back the plants and growing them in shortened light periods Schaffner caused such plants to show partial or in a few cases complete sex reversal. From these series of observations Schaffner is very positive in his conclusions that the heterozygous and homozygous chromosome condition has nothing to do with the determination of sex in hemp. From his studies in other dioecious plants he is even more firmly convinced of this fact. McPhee, noting that the male or female aspect of the plant is fixed from the beginning regardless of the environment, believes that the sex is determined in a Mendelian manner, but that the sexual expression may be modified by environment. The fact that seeds from female plants pollenized by pollen produced, under the influence of the environment, on the same plants give rise only to female plants would seem to substantiate the idea that the chromosome condition is the determiner for sex.

Hirata suggests that the Y chromosome has a tendency toward maleness, the X chromosome a tendency toward femaleness. The male tendency in Y over-

balances the female tendency in X so that a plant heterozygous for X and Y is normally male and an XX plant is normally female. In the autosomes the sexual tendencies are about equally balanced. The sexual determination is brought about by the excess respectively of the enzyme "andrase" for the male or of the enzyme "gynase" for the female. Under abnormal environment or under the influence of mutilation the dominant enzyme formation may be partially suppressed, allowing the opposite sex to express itself partially (intersexuality) or completely (sex reversal).

The writer believes that both views may be reconciled in the following manner. The sexual expressions as male or female are the result of different metabolic rates in the individual, as Riddle has suggested for the pigeon. A marked change in this metabolic rate from a higher to a lower rate or the reverse will change the expression of sex. If the change is to an intermediate metabolic rate the result will be the production of intersex forms. Under normal environmental conditions the determiners for the higher or lower metabolic rate are the sex chromosomes, hence the usual approximately equal numbers of males and females. Since this chromosome condition exists from the fertilization of the egg the embryo in the seed is already predetermined for a certain metabolic rate, i.e. for a definite sex. Hence we find that the plant will have the vegetative characters of a male plant or of a female plant from the beginning. If the external environment (light, moisture, etc.) is normal the plants will produce male or female flowers, respectively. Extensive mutilation will affect the metabolic rate, as will shortened daylight, infertile soil, etc. Depending upon the degree of this alteration there will be produced a few or many intersex flowers or even a complete sex reversal.

Sex reversal has been brought about by Schaffner in *Arisaema triphyllum* by simply transplanting the corms of male plants from poor, dry soil to rich, moist soil, or of female plants from rich, moist soil to poor, dry soil. An intermediate type of soil may produce monoecious plants with both male and female flowers in the same spathe. Hemp, *Arisaema* and *Carica* and other plants in which sex changes have been reported as a result of changes in environment or of mutilations are species which are as it were only sporadically dioecious in families or orders in which the normal condition is hermaphroditism or monoecism. Most of the Urticaceae (in the wide sense) are either monoecious or hermaphroditic. Even in *Carica papaya* perfect flowers are not rare and the nearly related plants (e.g. Passifloraceae) are hermaphroditic. Clearly sexual differentiation of the plants into male and female plants is not an ancient or very deep seated character. This is quite in contrast to the sexual condition in animals which is very ancient and deep seated. Even in the family Salicaceae we find intersexuality. Probably there are no families of flowering plants where the distribution of sexes in different individuals is deep enough to prevent partial reversal by environmental changes.

LIST OF LITERATURE

Bessey, E. A. 1928. Effect of the age of pollen upon the sex of hemp. *Amer. Jour. Bot.*, 15: 405–411.

Camerarius, R. J. 1694. De sexu plantarum, epistola.

Ciesielski, Th. 1911. Quomodo fiat, ut mox proles masculina, mox feminina oriatur apud plantas, animalia et homines? 1–15.

CORRENS, C. 1928. Bestimmung, Vererbung und Verteilung des Geschlechtes bei den höheren Pflanzen. Handbuch der Vererbungswissenschaft, 2: 1–138. 77 figures.

GREW, NEHEMIAH. 1682. Anatomy of Plants. *London.*

HIGGINS, J. E. 1916. Growing melons on trees. *Journal of Heredity*, 7: 208–220. 7 figures.

HIRATA, K. 1924. Sex reversal in hemp. (Preliminary report.) *Jour. Soc. Agric. and Forest. Sapporo*, 16: 145–168. Japanese with English summary.

———. 1927. Sex determination in hemp. *Journal of Genetics*, 19: 65–79.

LILIENFELD, F. 1921. Die Resultate einiger Bestäubungen mit verschiedenaltrigem Pollen bei *Cannabis sativa*. (Zur Kritik der Versuche von Th. Ciesielski). *Biolog. Centralbl.*, 41: 296–303.

MCPHEE, H. C. 1924. The influence of environment on sex in hemp, *Cannabis sativa* L. *Jour. Agr. Res.*, 28: 1067–1080. 1 pl. 3 figs.

MCPHEE, H. C. 1925. The genetics of sex in hemp. *Jour. Agr. Res.*, 31: 935–943.

PRITCHARD, F. J. 1916. Change of sex in hemp. *Journal of Heredity*, 7: 325–329. 1 fig.

SCHAFFNER, J. H. 1919. Complete reversal of sex in hemp. *Science*, (N.S.) 50: 311–312.

———. 1921. Influence of environment on sexual expression in hemp. *Bot. Gaz.*, 71: 197–219. 1 pl. 1 fig.

———. 1924. The influence of relative length of daylight on the reversal of sex in hemp. *Ecology*, 4: 323–334.

———. 1926. The influence of the substratum on the percentage of sex reversal in winter-grown hemp. *Ohio Journal of Science*, 25: 172–176.

———. 1927. Sex and sex-determination in the light of observations and experiments on dioecious plants. *Amer. Nat.*, 61: 319–332.

LIGHT AND SEXUAL CYCLES IN STARLINGS AND FERRETS

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DURING the years, 1926–28, at Trinity College, Hartford, the writer, with Morton H. Chapnick (1, 2, 3), studied and described the normal sexual cycle of male European starlings (*Sturnus vulgaris*) from birds killed at approximately fortnightly intervals and checked this study by repeating for a second year. An attempt was made to correlate the observed changes in the testes with environmental factors such as temperature, barometric pressure, and daily hours of daylight. With the equipment available, it was impossible to measure variations in light intensity over these periods or to follow changes in type and quantity of food consumed by the birds. Of all the environmental variables tested or ascertained in connection with this study, daily hours of daylight increase and decrease uniformly each year, so that the same dates in successive years have similar periods of daily daylight, though intensities vary from year to year. The conditions of the testes of the birds underwent changes which were surprisingly similar in the two years studied. Temperature and barometric pressure varied very irregularly and the testis changes appeared to bear no consistent relation to either of them.

The writer therefore proceeded to an experimental study of the possible relation of the ebb and flow of the tides of testis activity to the waxing and waning of daily light periods.

About this time, Professor Wm. Rowan (4), of the University of Alberta, Canada, working with Juncos, showed that seasonal migrations of those birds were correlated with the seasonal changes in the sexual conditions of the birds and these in turn with the daily hours of daylight to which the birds were exposed. His experiments led to the conclusions that the birds migrate if their sex glands are either increasing or decreasing in size and activity; but that they fail to do so if the sex glands are at either their maximum or minimum phases of the sexual cycle. He is continuing with his investigations of the problem of this relation of migration to sexual cycles and to seasonal variations in duration of day, using changes in daily period of illumination as his modifying factors.

IS LIGHT OR EXERCISE THE CONTROLLING FACTOR?

Owing to some experimental results obtained with a few birds during the spring migration period, subjected to enforced exercise for considerable periods after dark, without increased light periods, he concluded that it is not the increase of daily periods of light, as such, that induces increased sexual activity in the birds in spring; but the longer periods of muscular exercise daily, permitted by the lengthening days, that leads directly to the spring increase in germ-cell or sexual activity of the Juncos (4, 5).

In beginning the experiments on star-

lings, Professor Rowan's hypothesis as to the cause of changes in the sex glands was taken as a working hypothesis, though it did not seem to be proved beyond question that exercise was the factor really concerned, instead of light as radiant energy. His conclusions did not seem to be the only ones compatible with his data. Alternative explanations were therefore tested. Apparatus modelled after his, with alterations to increase its effectiveness, was used to cause the birds to be disturbed from their roosts every 20 seconds, for definite periods after nightfall. By testing the effects of 6–7 hour periods of this added work against those of equal periods of electric light from 60 watt bulbs and against controls, without added work or light, it was found that, in the months from December to April inclusive, added light was a very potent agent in inducing sex-gland activity, including spermatogenesis, in the starling. On the other hand, added work periods without added light were not only not effective in inducing spermatogenic activity, but tended to reduce both the size of the testes and their germ-cell activity.

However, by modifying the experimental method and the previous condition of the birds used, it was found that increased exercise periods led to a lag in onset of light-induced changes in the testes, whether those changes consisted of increase of activity induced by increased light exposure, or of decrease of activity induced by decreased daily exposure to light. This lag in onset was usually more than made up for later, by increased acceleration of the testis changes, induced by changes in exposure to light.

Light exposures after sundown, up to 6–7 hours per night, led to complete spermatogenesis and maximum testis size in 4–6 weeks at any time from December to April, while controls, kept on daily light periods similar to those of winter in duration, did not come into activity even in April, May, or June, when, in nature, the testes are at their maximum of activity and size. The testes of birds on forced exercise periods added to short or winter-length daily light periods, became smaller in size and less active in spermatogenesis than those of controls without either added light or exercise periods. The state of activity of the testes (and of ovaries, as judged by gross inspection) could be modified at will, in either direction, within the limits of the natural changes, by increasing or decreasing the daily periods of illumination. Birds could also be kept, for a month or more, in a condition of partial regression, by holding constant the daily periods of illumination and exercise (7).

THE EFFECT OF WAVE-LENGTH

Further studies, in 1928–1931 (8, 9, 10, 11, 12), with aid from the Committee for Research in Problems of Sex of the U. S. National Research Council, showed that the degree of stimulation of testis activity varies with the intensity of the illumination used and depends also on the color or wave-length of the light. Red was found to be highly stimulating, while green of the same luminous intensity was not stimulating but somewhat inhibitory to testis activity and to that of ovaries. Violet light, of low luminous intensity, was apparently slightly inhibitory as compared with lack of illumination, within the limits of the experiment.

Daily period, intensity, and wave-length of light reaching the birds were factors in controlling the seasonal sexual cycle in starlings, when the diet was kept adequate, varied, and rich in vitamines, proteins, fats, and carbohydrates. No mating nor egg-laying was observed in any of these experiments, even in birds brought to com-

plete sexual maturity, as judged by histological examination. These reactions seem to be controlled by factors outside the conditions operating in these experiments, and not by those inducing complete gametogenic fitness for breeding, if this fitness is judged from histological conditions alone.

Experiments also indicated that the maximum effect and consistency of results were to be obtained by large and immediate increases in periods of illumination to a maximum, rather than by gradually increasing periods. Filtered red light of 1.7 foot candles luminous intensity, acting for 6 hours per night after a 9½ hour daily daylight period in a basement room, induced approximately complete spermatogenesis in 23 days, in December and January. Green light of equal intensity caused slight regression even from the normal mid-winter quiescent state, in a great majority of cases.

In the study of the normal sexual cycle of these birds (3), it was noted that regression of the testes invariably set in before June 15, while the daily periods of illumination were still increasing in duration and intensity. Experimental analysis indicated that with red light, or even with artificial midsummer mid-day sunlight added to red light of proven potency, birds invariably passed the climax of testis size and activity, and underwent regression; that this regression was more or less independent of the proportions of ultra-violet or of green in the light used; and that it was probably due to the "throwing out of gear" of some part of the sex mechanism. It was impossible to maintain maximum testis size and activity indefinitely, even on the most stimulating exposures to light used. The data indicated that the time occupied by any phase of the sexual cycle bears an inverse relation to the effectiveness of the light stimulus (11).

A further grant from the Grants-in-Aid Committee of the National Research Council enabled the writer to study at Cambridge, to extend these studies on the starlings, and to try the effects of similar light exposures upon mammals with similar types of sexual periodicity. An unsuccessful attempt was made to determine whether the light entered the birds through the heads, because, on the reduced diet used, and with the handling of the birds twice daily to put on and remove hoods from half the birds in a cage, all the birds in the cage died before the results were evident. However, some birds were kept successfully on a diet restricted to "middlings" mash, low in proteins, fats and vitamines, under treatment with red and green lights, of previously proven potency, for over 22 days. On this diet red light did not induce marked testis activity, as it had done previously on adequate and mixed diets, and green was, as before, inhibitory. This result was taken to indicate that restricted diet may act as a limiting factor in the induction of sexual activity by stimulating exposures to light (Unpublished data). On the adequate diet previously used, similar red light, of somewhat less intensity, induced complete spermatogenesis in 20–23 days (9, 10, 11). These results indicate that, if either the light exposures or the diet be too restricted, sex-gland activity fails to occur. This may throw some light upon the sexual cycles and reactions of birds in the tropics, as these may be related to the seasons and to food and light changes.

As these studies stand, both light and diet appear to be factors in controlling sexual cycles in starlings—light, however, much more than diet. These experiments also indicate that the differences in effects induced by red, green, and white electric lights, with or without ultra-violet, are due to wave-length specificity, and not to the heat intensity to which the birds

are subjected by the exposures to light (9, 10, 11, 12).

EXPERIMENTS ON FERRETS

Ferrets were chosen for work at Cambridge, as the mammal most suitable for an investigation of the relation of light to sexual cycles in mammals, partly because the female sexual cycle of that animal has been so thoroughly studied by Drs. Marshall and Hammond of the Institute of Animal Nutrition of the School of Agriculture there, and partly because the swelling of the vulva of the female signals the coming into oestrus of the animal. No attempt has yet been made to analyse completely, or even very thoroughly, any of the aspects of the problem; but the effort has been made to find out the general possibilities and the amount of plasticity of the ferret as experimental material, in this connection. The experiments have been preliminary only, and the numbers of animals used in the various modifications of the light exposures have been small (35 in all). It was desired to find out if the sexual cycles of both sexes could be modified at will, in the direction both of complete oestrus and spermatogenic activity and of complete cessation of activity or anoestrum. All the experiments reported on, for this animal, are open to the objection that the numbers used were small and the results, therefore, inconclusive from a quantitative standpoint. This limitation of the work must be kept in mind while the report and discussion proceeds.

As pointed out above, the sexual cycle of the female ferret has been thoroughly studied by Dr. F. H. A. Marshall (13) and Dr. John Hammond with Dr. Marshall (14), of the Animal Nutrition Institute at Cambridge. That of the male ferret has been studied by Miss Marjorie Allanson of King's College, London (15). These cycles resemble those of starlings sufficiently to make studies on the ferret comparable to those already made on starlings, and described above. The swelling of the vulva of the female ferret indicates when she comes on heat,—a great convenience in such studies. Effective copulations, as to time and duration, were taken as criteria of activity of males at first. That this was none too good a test has since been discovered.

Experiments were begun on October 12, 1931, by subjecting three male and three female ferrets to electric light, after dark, from a 200 watt bulb, at such a distance as to throw light directly on the ferrets whenever the light was turned on. Luminous intensity ranged from 14.1 foot candles, at the front of the top cage of each row, to 4.88 foot candles at the back of the lowest cages. This light was turned on for 6–6½ hours each night after sundown, by a time switch, and light was freely admitted to the room during the day through a large window facing the cages. Two males and five females were kept as controls in a similar room across the hall, with similar temperature, food, and care, except that the light-treated animals were denied nesting boxes and given too little shavings to permit them to hide from the light. This prevented them from keeping as warm as the controls.

Two of the experimental males died on November 18th and 25th, after 37 and 44 days of exposures to electric light. The cause of death of one was unknown,—possibly distemper. The other died from abscesses in the throat and top of the head. These illnesses were not likely to increase the effects of the light treatments, but rather to retard them. So the testes were taken for study. One of the control males was transferred to the lighted room in place of one of those that died, leaving only one control male. Neither room

was artificially heated and the experimental animals were kept colder than usual, or than the controls, by being deprived of excess shavings.

By November 23rd, (42 days) two of the three females were on heat and the third was found to be hiding from the light by burying in the shavings. She did not come on heat till after the shavings were reduced on December 1st, reaching complete heat by December 20. These three females were mated with the original light treated male on December 10, 11, and 21 respectively. They became pseudo-pregnant and underwent all the changes usual to this condition, such as shrinking of the vulva, enlargement of mammary glands and teats, darkening of the areola round each teat, and shedding of some fur. Since ovulation and pseudo-pregnancy occur, in the ferret, only after prolonged copulation, these changes were taken as evidence of ovulation. Whether the ova shed at these times were normal and capable of fertilization, or not, remains to be tested. No sperms were found in the fluid from the vulvae of these females after these matings. A motile fluid with flagella-like bodies, presumably from the epididymis, and epithelial cells, normal for oestrus, were found.

On the male side, the two males that died had undergone some stimulation of germ-cell multiplication and considerable interstitial cell increase. Epididymides were modified considerably in one and not in the other. Comparison was made with conditions in testes and epididymis from a male bought from a dealer and killed on December 12th, without light treatments. These two males had not been tried with females in oestrus, because previous to their deaths none of the females were yet in oestrus, or the males were too ill to bother with them. The other light treated male showed marked libido; his testes were enlarged, and had moved posteriorly, from the winter position in the groin, to the bottom of the scrotum below the anus, where they protruded, and the hair over the scrotum had begun to thin out. He mated successfully with all three females as above described. On December 22, the day following a copulation lasting one hour and forty minutes, he was sacrificed, and his reproductive organs, pituitary, thyroid, and adrenals were taken and fixed for study. No sperms were found in his epididymis, nor in the seminiferous tubules. The latter were enlarged, as compared with those of the normal ferret killed on December 12th, and more germ-cell generations were found. Interstitial tissue was much increased and the epididymis was like that of a normal breeding ferret except for the lack of sperm contents (16).

The libido of the male transferred from the control to the light room on November 25th was quickly stimulated so that he tried persistently to copulate.

On December 7, 12 and 15, more males and females were added to both control and experimental rooms and their light exposures measured as to time and intensity; since it was evident that ferrets are susceptible of modification of their sexual cycles by changes in amounts of exposure to light, somewhat as the starlings are.

All light treated females of the new additions as well as those three of the first (pseudo-pregnant) group, so treated, came into oestrus and were mated with light stimulated males on February 2, 3, 8, 12, 17, 18, 29, and March 1, except one of the first three, which came into oestrus on March 12 and was not mated. She was kept in oestrus to see how long she would stay so. She remained in oestrus, as is usual with unmated females in summer, till after her daily period of exposure to light was reduced from about 18 hours to

about 16 hours per day, when she went off oestrus and her vulva shrank toward winter condition in May.

Pseudo-pregnancies again resulted in the cases of all these matings, except that on March 1, which led to a litter of 8 young, born on April 11, (unfortunately only 3 days earlier than the earliest litter obtained by Marshall and Hammond in their studies of pregnancies and pseudo-pregnancies in ferrets) (14).

Motile sperms were found in the fluid removed from the vulva or vagina after copulations from February 8th onward; but the numbers were small and their motility low till matings on February 29th. This low concentration and feeble motility would account for the failure of fertilizations and so for pseudo-pregnancies instead of real pregnancies, on those dates. Even in summer, a low concentration of sperm, in the smear from the vulva after copulation, is associated with pseudo-pregnancy only (14).

Some of these females again came into oestrus in April and were transferred to the control room with the daylight period reduced to about 7½ hours per day. They went off heat, even in this, the normal, period of heat in ferrets. Between October 12th and April 1st, no control female showed any sign of coming into oestrus, though all the experimental females had been pseudo-pregnant at least once, and some three times, before April 15.

The original control male, kept on short light schedule, showed little or no interest in females in complete oestrus and made no real attempts to copulate with them. Light-treated males copulated, whether they were fertile or not. They were potent; he remained impotent, on the short days, even up to March 21st when he was sacrificed and sperms were found in his testes, which were in complete spermatogenesis. His epididymides were full of sperm, and his testes large. An experimental male killed at the same time was in somewhat the same condition of testes and epididymides. So were males recently bought, and put on light treatments for 10 days or on short days for 28 days respectively. A study of these testes has not yet been completed except to ascertain that all were at complete spermatogenesis. Whether the light treatments cause males to produce sperms any earlier than is normal has not yet been learned.

To test whether or not the light causing these changes is received through the head and eyes or through the general body surface, four female ferrets from the control room, with previously restricted daily light exposures, and showing no signs of heat or oestrus, were moved to the light room on March 4th. Two of these were hooded each night, from 4 P.M. till 9 A.M., with black velvet hoods covering the whole head and tied behind the ears,—during the time the light was turned on, as well as part of the daylight exposure period. The other two, placed in exactly the same relation to the lighting systems, were not hooded, but received the light over their whole bodies. The previous light history of these two pairs of ferrets had been the same. The two unhooded ferrets came on full heat by April 9th, were subsequently mated and pregnant. Of the hooded animals, one showed no sign of coming on heat at all till she died on May 8th, from tuberculosis; the other showed first signs of vulval swelling on April 14th, but did not reach complete oestrus till May 18th when she was mated with a black ferret and with a white one the following day. Her coming into complete oestrus was slowed up by a reduction of the daily exposure to electric light by one hour on May 5th. These two hooded females were slower in coming into oestrus than females kept in the control room behind curtains for the same periods each night, and receiving no electric light after dark. Some

light filtered round the edge of the curtain and could be picked up by those animals behind the curtain, if they focussed their eyes upon the beams, so passing the curtain. Other modifications of the periods of exposure to light have been tried and the results are consistent with those above described. They will be included in the description of the study in detail, to be reported elsewhere, when finished.

It is enough to say here that increasing intensity of illumination, as spring advanced, during the 7½ hours when the ferrets on restricted exposures were receiving light, caused female ferrets to come into oestrus, while at the same time a reduction, of one to two hours, in the period of added electric light, received by ferrets on a total exposure of about 18 hours per day, resulted in females going out of oestrus without being mated, after they had been brought to the full oestrous condition by such long exposures.

These results lead to the tentative conclusions that increase of either duration or intensity of the daily periods of exposure to light or of both, causes increased sexual activity in female ferrets, leading to complete oestrus, in time; in male ferrets, it induces some increase in germ-cell activity and great increase of interstitial cell mass and, probably, of activity, with increase of libido and the production of a condition of the epididymis similar to that of the normal breeding ferret. Reduction of either period or intensity of the exposure to light leads to an anoestrous condition, in females, and to loss of libido and of testis size, in males. The exact reactions of males to these changes require much further study.

IS THE HYPOPHYSIS INVOLVED IN THE REACTION?

Results obtained by others, after treating male and female mammals with anterior lobe pituitary substances, and particularly those of Hill and Parkes (17), in London, with ferrets, lead to the strong suspicion that the anterior lobe of the hypophysis is involved in these reactions. But further study is needed before one can offer any very complete or definite theory as to the mode of its action. It appears probable that the light rays, of the long-waved sort, react upon some part of the head of the ferret and, through that receptor, upon the anterior lobe, to stimulate it to increased secretion or liberation into the blood stream of the hormone which causes increased gonadal activity, and that this increase leads to activity of the secondary sex mechanism involving the uterus, vagina, vulva, and behaviour, in females, and the epididymis, penis, and behaviour, in males. Whether this receptor is confined to the eyes or to the naked skin of the face and ears has not yet been ascertained. Ferrets with cataract or opaque lenses react in the same manner as those with normal eyes. So that, while one may suspect the eyes as the receptors, a clear image is not necessary to the effect. More than that, sleeping, and very inactive ferrets react just as well as active, wakeful ones. This suggests that whatever part of the spectrum is effective in ferrets must penetrate at least the skin of the eyelids before reaching the receptor proper, which mediates the action to the sex mechanism. A neuro-humeral effect, of the sort described by Parker (18), is suggested.

Different parts of the spectrum have not yet been tried with ferrets; but the necessity for ultra-violet is excluded by the fact that all these ferrets were behind ordinary window glass throughout the experiments. From the results with starlings, one is led to suspect the long-waved red light as effective with ferrets also. But it is quite possible that some region other than that effective in starlings may be the one most potent in modifying the sexual cycle of the ferret.

Studies on the relations of daily period of exposure to light to sexual activity and to seasonal sexual cycles in a mammal have been made by Baker and Ranson (19), of Oxford, England, using voles as experimental material. These studies lend support to our findings with ferrets, that the female sexual cycle is conditioned to a great extent by seasonal variations in daily exposure to light, while that of the male is less so. They also used electric light under controlled conditions. They have found, in addition, that type of food plays a considerable part in the reaction. In that they agree with our findings for starlings.

All the studies referred to above indicate that seasonal sexual cycles in, at least, some birds and mammals, are conditioned to a very considerable extent by seasonal changes in the duration and intensity of the daily periods of exposure to light of the visible or long-waved sort, and that, in birds at least, red light is more effective in this respect than shorter waved light. In birds, both sexes appear to be equally dependent on variations in exposure to light for their seasonal changes of sex-gland activity. In the mammals investigated, females are much more completely controlled in this way than males, under the conditions of experiment so far used. It is increasingly apparent that diet also affects the reactions of birds, at least, to the light induced changes and that it may even act as a limiting factor in this respect. This may very probably be because of deficiency in vitamines and proteins already known to be essential for normal reproductive rhythm, and capacity.

The whole problem requires, and would seem to be likely to repay well, much further study under well controlled conditions. The fact that the anterior lobe of the pituitary seems to be involved in the reaction as a mediator of the effect upon the sexual apparatus indicates the need for coöperation of those engaged in the study of sexual photoperiodism with the numerous students already so far advanced in the study of the intimate correlation of the activities of the anterior lobe of the hypophysis, the gonads and other sex apparatus, and of the thyroid and adrenals as also likely to be involved. This has been discussed elsewhere in more detail (11, 12, 16).

LIST OF LITERATURE

(1) Bissonnette, T. H. 1930a. Am. Jour. Anat., 45: 289–305.

(2) Bissonnette, T. H., and M. H. Chapnick. 1930. *Ibid.*, 45: 307–343.

(3) Bissonnette, T. H. 1930b. *Ibid.*, 46: 477–497.

(4) Rowan, Wm. 1925. Nature, 115: 494–5.

——. 1926. Proc. Boston. Soc. Nat. Hist., 38: 147–189.

——. 1929. *Ibid.*, 39 (5): 151–208.

(5) ——. 1928. Nature, 122 (3062): 11–12.

(6) ——. 1930. Proc. Nat. Acad. Sci., 16 (7): 520–525.

(7) Bissonnette, T. H. 1931a. Jour. Exp. Zool., 58: 281–319.

(8) ——. 1931b. Physiol. Zool., 4 (4): 542–574.

(9) ——. 1932a. Physiol. Zool., 5 (1): 92–123.

(10) Bissonnette, T. H., and A. P. R. Wadlund. 1931. Jour. Morph., 52 (2): 403–427.

(11) ——. 1932. Jour. Exp. Biol., 9 (4): 339–350.

(12) Bissonnette, T. H., and A. P. R. Wadlund. 1933. Bird Banding, January. 4 (1): 8–18.

(13) Marshall, F. H. A. 1904. Quart. Jour. Micr. Sci., 48: 323–346.

(14) Hammond, J., and F. H. A. Marshall. 1930. Proc. Roy. Soc. B., 105: 607–637.

(15) Allanson, M. 1931. Jour. Physiol., 71: 20.

——. 1932. Proc. Roy. Soc. B., 110: 295–310.

(16) Bissonnette, T. H. 1932b. Proc. Roy. Soc. B., 110: 322–336.

(17) Hill, M., and A. S. Parkes. 1930. Proc. Roy. Soc. B., 107: 39–49.

(18) Parker, Geo. H. 1931. M. B. L. Collecting net, Woods Hole, 6 (4): 93, 96–100.

——. 1932. Humoral Agents in Nervous Activity, with Special Reference to Chromatophores. Cambr. Univ. Press. 79 pp.

(19) Baker, J. R., and R. M. Ranson. 1932. Proc. Roy. Soc. B., 110: 313–322.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

WARNING COLORS AND MIMICRY

Being a review of *The Zoological Society's Expedition to the Zambesi, 1927. No. 4. On the Ecology of Tree-frogs in the Lower Zambesi Valley, with special reference to Predatory Habits considered in relation to the Theory of Warning Colours and Mimicry*, By Hugh B. Cott. *Proc. Zool. Soc. London*, 1932, Part II (July), pp. 471–541, Pls. 1–2.

By W. L. McAtee, Cherrydale, Va.

One certainly must have the true religion to uphold selectionist doctrine relative to the so-called protective adaptations of animals. If we may judge from current practice, he must accept the most tenuous whimsicalities of his forbears as if they were respectable theory and he must so far abdicate his intellectual integrity as to make assertions that do not agree with his own data, much less with the observed facts of nature. In other words to be a good selectionist, he must stultify himself at every turn.

The latest example is furnished by Hugh B. Cott, a disciple of that arch-selectionist Professor E. B. Poulton of Oxford University whom he profusely thanks.

In publishing on the tree-frogs of the Lower Zambesi Valley, this author mixes with the warp of fact derived from collected specimens the woof of stereotyped selectionist phrasings, which to change the metaphor but not the word is simply woof, woof!

Speaking of a boldly brown and white striped tree-frog (*Megalixalus fornasinii*), he says (p. 475) "To human eyes at any rate, the creature ceases to bear any marked resemblance to a frog," while at the same time he publishes illustrations that show quite clearly it does look like a frog. He goes on to say that posture (which by the way is just like that of other tree-frogs the world over), and pigment combine to distract the observer's attention and effectively to mask the identity of the frog, while a few pages previously he informs us that he collected within 24 hours of his arrival 802 frogs of which 381 were of this species, and 289 of three other kinds together.

He is convinced that the creature benefits in being enabled to capture more alert prey "because its attitude and 'ruptive' colour scheme combine to take away its frog-like appearance." (p. 476). What matter to its victims whether it is frog-like or unfrog-like? It is one of the things that gets them and if they react defensively at all, it would be in relation to what the frog is—an enemy—without regard to kind.

Of its prey, he mentions dragon-flies, grasshoppers, muscid flies, and Lepidoptera as alert and most difficult to capture and says they were "eaten in conspicuously greater numbers" by *Megalixalus* than by the other frogs. The dragon-flies according to his tabulations were damsel-flies, the weakest of their group, most of which can be picked up with the fingers as they hang, wings together, from the tips of grass blades or other perches, and which on the wing are feeble flutterers. The grasshoppers while good jumpers must by no means be difficult to capture as practically all insectivorous predators feed upon them. The statement that they are eaten

in conspicuously greater numbers by this frog than by any of the other species examined is untrue, as 7 Acrididae were found in 360 stomachs of *Megalixalus*, or 1 to each 51.4 stomachs, while 3 were found in 122 stomachs of another frog (*Hyperolius argus*), or 1 to each 40.6 stomachs. Mosquitos are included by Cott in his table of prey difficult to capture, but it is very unlikely that these small fragile insects offer the least difficulty to tree-frog predation. Probably all that is necessary is that they come within reach. The Lepidoptera found in the stomachs of this frog were more than half larvae or caterpillars, mere "worms" to which the terms "active, alert, rapid in flight" most assuredly do not apply. What difference does it make anyway as to whether prey is alert, quick on the take-off, etc., if the mode of feeding, as it is in most frogs, is a lightning-like flick of the tongue that gives no time for alertness to function? The whole argument relative to advantage of this frog in relation to prey is special pleading with little regard to facts but just what would be expected from a faithful disciple of Selectionism.

Cott, while dilating on the powers of *Megalixalus* in capturing prey "active, alert, rapid in flight," says nothing about the much greater prevalence in the food of this frog of the feeble and partly wingless plant lice. He has nothing to say also as to why this frog fed to a considerably smaller extent upon ants (very "specially protected" insects) than did any of the other species. The average scientist viewing these things in a normal way would assume that because of special habitat, size, or other factors *Megalixalus* simply finds it convenient to subsist upon a somewhat different assortment of prey from that taken by the other frogs. That is about all there is to it, and in this effusion, as in many others perpetrated by selectionists, much good white paper has been needlessly dirtied by extended fantastic speculations about happenings, which if viewed in a more moderate and logical way would call for no special comment.

Warning colors are given a flourish in this Zambesi paper and are said to be associated with defensive skin secretions. The frog (*Hyperolius argus*) about which this point is made has the sexes of very different color patterns, the female being allegedly conspicuous although the picture presented would lead one to think it a fine selectionist example of concealing coloration. The male with presumably the same skin secretions is plain. These inconspicuous males, however, are found in the same situations as those favored by *Megalixalus fornasinii*, the most conspicuously colored frog of the entire collection.

To sum up these arguments, the most strikingly colored (broadly brown and white striped) frog the author treats is held to illustrate the "disruptive" type of concealing coloration, while one which is brownish with "eye-spots" almost matching some of the holes on a leaf on which it sits, is said to have "a colour pattern that is at once striking and distinctive" (p. 477), i.e., warning, and the author ventures to predict that these "frogs will be found to possess some defensive secretion which renders them undesirable as food" (p. 478).

The plates illustrate four species of frogs, one plain green, one brownish with orange ocelli, one finely striped yellow and black, and one broadly striped brown and white. All are said to be protected in one way or another. The appetite of the selectionist for "protectedness" is as insatiable as it is indiscriminating. Plainly, the motto is "Whatever is, is right," and the attitude of mind differs in no essential from that of the special creationist, whose position Darwin was so at pains to challenge. Were Darwin alive now, he would have the mortification of seeing what are said to be his ideas held as dogmas, and accepted with an unwavering faith and promulgated with a fanatical zeal which have no part in science.

The truth is that acrid or poisonous skin secretions are of common, perhaps of universal, occurrence among frogs and toads. Some of these animals are plainly, others conspicuously, colored, but what of it? The group exhibits a great variety of color patterns and almost every imaginable intergradation thereof. But must each be held significant, a definite meaning asserted, and a highly theoretical explanation of it be made in every case? Em-

phatically no; adaptations that apparently will serve in one case, in another will not; in endeavoring to explain them all, the whole effort becomes a hodge-podge of error, misconception, and misstatement that only the stoutest can stomach.

Cott says on a single page (and even these fallacies are not all that can be gleaned there):

> The adaptive significance of colour in frogs has been little studied in the past, and I am persuaded that research will prove that colour and pattern play a much more important part in frog-ecology than is generally imagined. . . .Poisonous skin secretions are of common occurrence among the Anura. In many species they are known to furnish an effective means of defence against predatory enemies. . . . Snakes and birds, the principal enemies of frogs, depend largely upon vision in hunting for prey. There is evidence that these enemies learn to discriminate between poisonous forms and those which are good to eat. (p. 478).

These extracts make a very good one-page record of assumption, misstatement, and error even for a selectionist. He is persuaded that colors are important in frog-ecology, but self-persuasion in the lack of evidence is something entirely out of place in science. "In many species," he says, "poisonous skin secretions are known to furnish an effective means of defence." If the word *many* is taken at its ordinary valuation, this is a definitely untrue statement. Take the next remark, that snakes and birds learn to discriminate between poisonous forms (of frogs, by implication) and those which are good to eat. There is no evidence of any frog being dangerously poisonous either to snake or bird predators upon it, hence the discrimination alleged is a myth.

The author notes that snakes are very abundant in the region of the study, and goes on to say: "Tree-snakes are undoubtedly their [i.e. the frogs'] greatest enemies. Tree-frogs are never beyond the reach of these silently gliding forms. . . . From such there is no safety" (p. 483). This controverts what he has previously said about concealing coloration of the frogs, and paradoxically is further an example of the horrific statements made by selectionists to show the severity of the struggle for existence. The other side of the picture, conveniently forgotten here, is given on p. 474, where it is said of tree-frogs: "Such is their abundance, that in suitable localities . . . a systematic hunt will yield a frog every yard or two. If we calculate the population of such an area in terms of one tree-frog per 4 square yards, or say, 1000 per acre, it is probable that this would not be an over-statement." To the non-selectionist it would appear that where there is a population of 1000 per acre, tree-frogs cannot be experiencing a very severe struggle for existence.

One of the loveliest things about being a selectionist is that the traditions of the school permit argument with entire disregard of the facts. For example, hear Cott on protected insects. After mentioning some lizards that feed upon ants, he says: "But although the adaptations fall far short of perfection, and in some cases prove ineffectual in defence, facts such as these in no way disprove their general usefulness."

It seems futile to present statements of fact to writers of this type. Bequaert (*Bul. Amer. Mus. Nat. Hist.*, Vol. 45, pp. 271–331, 1922) has catalogued and discussed the predatory enemies of ants from spiders to man and says: "There is certainly little or no evidence to show that, as the theory is often expressed, ants are unpalatable to most insectivorous animals and are merely eaten accidentally or during the time in which young birds or other animals are learning what to eat with impunity and what to reject.' "

McAtee furthermore summarizes (*Smiths. Misc. Coll.*, Vol. 85, No. 7, 1932, p. 96) information about ant enemies, concluding: "In fact it would be difficult to name a group of insects that is so thoroughly preyed upon as the ants, and impossible to name one that has so many specialized foes scattered through the various animal phyla."

Despite Cott's assertion, the fact is that there is no "general usefulness" of adaptations of ants in relation to predators. The latter take all the ants they want, and the ant supply remaining plentiful proves nothing beyond the fact that there are too many to be eaten up, or for that matter even reduced in numbers.

Cott quotes experimental results tending to show that protected insects are eaten only up to a certain point and not beyond it. This merely indicates satiety, not pro-

tection. A man can eat beefsteak until it palls upon him, but still have an appetite for pastry, and perhaps even for ice cream and candy after that. The reverse, however, is just as true, for, granted a fresh start, after being cloyed with candy, he can again relish beefsteak. Just because a man or a bird does not keep on eating the same item of food indefinitely does not justify the assumption that the food is distasteful (or protected). The whole of the experimental evidence as to edibility of prey is scarcely worth the paper it is printed upon, a fact pointed out by McAtee twenty years ago (*Proc. Acad. Nat. Sci. Phila.*, June 1912). Animals do not react naturally in captivity, they eat things never encountered in life, and they refuse things customarily eaten by their wild brethren. Drawing conclusions as to their natural tastes from abnormal behavior in captivity is entirely unjustifiable. The citing of any amount of experimental evidence as to choice of food leaves the student of the natural feeding habits of animals entirely unmoved.

Cott goes on to say: "An animal is compelled by hunger to eat unpalatable food. If the preferred article is not present, the next best must be taken" (p. 494). This is an absolute misconception of the process of food finding. Animals take what is most available at the particular time and place. Availability of course is qualified by the size of the animal in relation to possible prey, specializations as to food, etc., but in general availability means abundance, and feeding proceeds from the more to the less available items, not from imaginarily preferred or palatable, to the less preferred or unpalatable things. No one who has studied the food habits of wild animals can doubt that availability is in general the controlling factor in choice of food.

A further Cottism (Poultonism by inheritance of course) follows: "It is now fairly well established that an animal's knowledge of what insects are good to eat and what are not has to be acquired in the light of individual experience." There is practically no such distinction as insects good, and not good to eat, for the evidence indicates that all are eaten more or less in proportion to their numbers.

Cott presents a graph (p. 532) and a Table XIV on which it was based showing the food preferences of four species of tree-frogs, of which he says, "I think it can hardly be doubted that the figures in Table XIV point to the conclusion that frogs are not such indiscriminate feeders as is often supposed, that they learn from experience what food is palatable and what is to be avoided, and that they exercise some choice in the manner of diet. It is difficult to explain the facts in any other way."

Considering the way the curves in the graph for three species of frogs are almost superimposed, and that the fourth diverges notably with respect to only two food items, it is clear that we are reading a record of availability, and that the frogs were feeding more or less indiscriminately on what was available to them.

Cott himself concedes as much in a statement on p. 526 where after commenting on the relatively enormous feeding capacity of the tree-frogs he says: "although these creatures do hunt actively in search of food, especially in the evening, yet they are far less active and mobile than many of the insects upon which they feed, and they therefore must rely upon, and make use of, whatever suitable prey happens to come within their reach—the stomach functioning as a kind of reservoir, ever ready to receive food that chance incidents may render available."

Despite all the evidence as to practical indiscriminacy among prey available to them, the author concludes that tree-frogs are selective agents in the production of warning colors and mimicry and says that analysis of stomach contents lends indirect support to this conclusion. Let us consider briefly the single item of ants; of 11,428 insects identified from about 800 frog stomachs, 9937 or 87 per cent consisted of ants. These insects were not only highly available, therefore, but they were eaten with the greatest freedom. Cott himself has to conclude that "there is little evidence that the defences of ants are in the least degree effective against the predatory attacks of batrachians," a conclusion which is equally true of numerous other groups of predators.

Ants, nevertheless, have always been

hailed by selectionists as aggressive, well armed, highly "protected" insects, and ant mimics have been recorded by the score. If there can be numerous ant mimics in the absence of a scintilla of evidence that ants are protected from predators, the theory of their origin by natural selection collapses, and the theory failing in such a case, it fails in all. Selectionists may ignore facts presented by their opponents but how they can forever ignore and misinterpret those presented in their own writings, can only be explained on the ground that their belief in natural selection has become a sort of religion. In fact we seem to have in selectionists the kind of people who before the day of Darwin would have been special creationists. They are just the same sheep even if in another fold.

BRIEF NOTICES

EVOLUTION

STUDIES ON THE VARIATION, DISTRIBUTION, AND EVOLUTION OF THE GENUS PARTULA. *The Species Inhabiting Moorea. Carnegie Institution of Washington Publication No. 410.*

By Henry E. Crampton. Carnegie Institution of Washington, D. C. $13 (paper); $14 (cloth). 9 x 11½; vi + 335 + 24 plates; 1932.

This is the third volume of Crampton's studies of the land snail *Partula*, the first having been devoted to the species of the neighboring island of Tahiti and the second to those of the Mariana Islands. The author's first exploration of Moorea was in 1907 and 1909, while in 1923 and 1924 the island was again explored in greater detail. In this short time changes in the varieties had occurred.

> In some instances varietal differentiation has gone forward with truly remarkable rapidity, and this process seems to be continuing to a noticeable extent. It would not be expected that the novel differences would amount in degree to distinctions of *specific* value, but they are the same in nature as such distinctions, and are to be regarded as actual steps in the direction of specific evolution.

The factors underlying this differentiation are, the author concludes, genetic in character. In some cases the evidence of mutation is unassailable, embryonic offspring being found in the brood-pouch of a parent from which they differ in the mode of coil. In no case is there evidence that environmental conditions are causes of organic differentiation. Certain species occur only in sharply restricted territories not marked off by any environmental peculiarities, while *Partula taniata* exists in association with all of these forms as one and the same species. Obviously it would be inconsistent to attribute the like qualities of the members of *Partula taniata* to supposedly similar circumstances throughout the island and at the same time to refer the distinctions of the other species to diverse external conditions.

The distribution of the species of *Partula* in the various Pacific islands is only explicable, the author concludes, on the hypothesis that the islands are the remnants of a vanished continent. The alternative theory of human transport of the snails from one island to another may account for some cases but not for most.

The book is illustrated with beautiful color plates of the shells and with photographs of the environment. There is, unfortunately, no index.

HUXLEY MEMORIAL LECTURES 1925–1932. *By E. B. Poulton, Sir Peter C. Mitchell, G. Elliot Smith, F. O. Bower, Graham Wallas, Sir Arthur S. Woodward, Aldous Huxley. Macmillan and Co., London.* 2s. 6d. net. 5¼ x 8¼; 172 (paper).

In 1925 the Old Students' Association of the Royal College of Science, with which Huxley had so long been associated, commemorated the centenary of his birth through a memorial lecture. The success of this determined the Governing Body of the Imperial College of Science and Technology to establish an annual lecture, of which the fruits of the first seven years are here gathered together. E. B. Poulton's biographical lecture on Huxley heads the list; Sir Peter Chalmers Mitchell points out the dangers of stretching a generalization from the known to the unknown;

G. Elliot Smith's lecture on "Conversion in Science" is largely given over to an exposition of his own diffusionist views on human culture; F. O. Bower considers "The Origin of a Land Flora;" Graham Wallas deals with the relation between physical and social science and the academic organization of student-research; Sir Arthur Smith Woodward with "Modern Progress in Vertebrate Palæontology;" while Aldous Huxley analyzes his grandfather's achievements as a literary artist.

THE GEOLOGICAL HISTORY AND EVOLUTION OF THE HORSE. *Geology, Leaflet 13.*

By Elmer S. Riggs. Field Museum of Natural History, Chicago. 40 cents. 5½ x 8½; 54; 1932 (paper).

This leaflet tells the familiar story of the evolution of the horse, based upon a comparison of the fossil remains of successive geological periods. The bony structure of the modern horse is first considered, as a basis for comparison. The history of the horse through the different geological periods is then outlined, after which modifications in the skeleton are traced in detail. Among the more important changes which are evident are: (1) an increase in size, the earliest horse, *Eohippus*, being no larger than a fox; (2) a change in the proportions of the head, especially evident in the jaws and teeth; (3) a change from a broad-footed, four-toed animal which walked on a pad beneath the toes, to an animal walking on a single toe with a broad hoof; (4) a change in habit from a lowland or woodland animal to a strong, swift inhabitant of the plains. There are nineteen plates, and a bibliography of fifteen titles. An excellent popular treatise, which should be particularly useful to high school and college teachers of biology.

THE MECHANISM OF CREATIVE EVOLUTION.

By C. C. Hurst. The Macmillan Co., New York. $6.00. 7¼ x 9¾; xxi + 365; 1932.

So numerous have been the discoveries of biology in recent years that the writer has gathered together the "multitudinous facts which go to make up the genetical story of creative evolution, lest essential synthetic values may be lost in a maze of detail." The rediscovery of Mendel's law and the rapid growth of this line of work has brought about a revolution in biology. An exact science, according to Hurst, has developed out of the discoveries concerning chromosomes and genes and their interrelations. He has brought all of these findings together in an impressive array. The book is abundantly illustrated with excellent figures and diagrams, has a lengthy literature list, and a detailed index.

URSPRUNG DER MENSCHHEIT. *Über den engeren Anschluss des Menschengeschlechts an die Menschenaffen.*

By Hans Weinert. Ferdinand Enke, Stuttgart. 21 marks (paper); 23 marks (cloth). 6½ x 10; xii + 380; 1932.

Beginning with Haeckel's *Anthropogenie* (first published in 1874) the author reviews critically the literature through 1931 concerning the evolution and origin of man. He arrives at the conclusions that the chimpanzee and *Homo sapiens* originated from the same anthropoid stock, which split off in the late Pliocene or early Diluvian period, and that the limits of man's Eden cannot be definitely defined. It probably includes Eurasia, possibly Africa. The book has a bibliography of 14 pages, and subject and author indices.

GENETICS

ON CERTAIN ASPECTS OF HUMAN BIOLOGY. *The University of Birmingham, Faculty of Medicine, William Withering Lectures, 1932. Lecture I. On the Genetic Significance of Hemilateral Asymmetry in the Vertebrate Organism.*

By C. J. Bond. H. K. Lewis and Co., London. 2s. 6d. net. 5½ x 8½; 38; 1932 (paper).

ON CERTAIN ASPECTS OF HUMAN BIOLOGY. *The University of Birmingham, Faculty of Medicine, William Withering Lectures, 1932. Lecture II. On the Making of Use Acquirements; the Neuro-Psychic and Other Responses.*

By C. J. Bond. H. K. Lewis and Co., London. 2s. 6d. net. 5½ x 8½; 44; 1932 (paper).

ON CERTAIN ASPECTS OF HUMAN BIOLOGY. *The University of Birmingham, Faculty of Medicine, William Withering Lectures, 1932. Lecture III. Genetics in Relation to Public Health and Preventive Medicine.*

By C. J. Bond. H. K. Lewis and Co., London. 2s. 6d. net. 5½ x 8½; 34; 1932 (paper).

ON CERTAIN ASPECTS OF HUMAN BIOLOGY. *The University of Birmingham, Faculty of Medicine, William Withering Lectures, 1932. Lecture IV. On the Influence of Environmental Conditions on the Shape and Constitution of the Red Blood-Cell. Lecture V. On the Clinical and Biological Significance of the Above Observations.*

By C. J. Bond. H. K. Lewis and Co., London. 2s. 6d. net. 5½ x 8½; 57; 1932 (paper).

A series of lectures planned for a rather general audience and covering a wide range of subjects. In the first lecture the author discusses the inheritance of asymmetry in animals and in man. Lecture II discusses the way changes occur in the cell structure and function which constitute what the author calls "Use-Acquirements." Lecture III gives a brief summary of human genetics and a program of eugenic reform. Lectures IV and V describe the results of research upon certain aspects of the physiology of the red blood cell.

VARIATION ET MUTATION EN BACTÉRIOLOGIE.

By J. G. Marchal. Librairie Le François, Paris. 50 francs. 6½ x 10; vii + 307; 1932 (paper).

The first fifth of this book is devoted to an historical account of researches on variability in bacteria, protozoa, and metazoa. In the remaining portion the author describes his own experiments on the production of temporary variation and mutation in single cells of bacteria by the use of various chemicals in culture media. He used *B. coli mutabile* Neisser, *B. caryocyaneus* Beijerinck-Dupaix, *B. pyocyaneus* Gessard, and *B. prodigiosus* Ehrenberg. He conducted these experiments with the hope that his results would throw more light on genetic mechanisms in higher organisms, but concludes that more work will have to be done to separate phenotypic and genotypic changes, before microbiology can contribute effectually to the general study of genetics. There is a bibliography of 18 pages.

INDIVIDUALITY OF THE BLOOD *in Biology and in Clinical and Forensic Medicine.*

By Leone Lattes. Translated by L. W. Howard Bertie. Oxford University Press, New York. $7.50. 5½ x 8⅝; xiv + 413; 1932.

This is a translation of a book which was first published in Italian in 1923. Later German and French editions were issued. In each edition the work has been revised and enlarged to keep abreast of the rapid advance made in the field. New matter has been coördinated with old and obsolete material eliminated. The main sections deal with (1) individual reactions of normal blood, (2) hereditability, (3) individuality of the blood as an ethno-anthropological fact, (4) individuality of the blood in its clinical applications, (5) individuality of the blood in forensic medicine, and (6) technique of the individuality reactions. The work includes numerous figures and tables, a bibliography of 2,375 titles, and author and subject indexes.

GENERAL BIOLOGY

ANTONY VAN LEEUWENHOEK AND HIS "LITTLE ANIMALS." *Being Some Account of the Father of Protozoology and Bacteriology and His Multifarious Discoveries in These Disciplines. Collected, Translated, and Edited, from His Printed Works, Unpublished Manuscripts, and Contemporary Records.*

By Clifford Dobell. Harcourt, Brace and Co., New York. $7.50. 7¼ x 9¾; vii + 435; 1932.

All things happen for, as well as to, him who waits. We have been wanting for a long time an adequate account of the life and labors of Antony van Leeuwenhoek. Paul deKruif's chapter in *Microbe Hunters* about him was good, but only as an appetizer. What was needed was a good, solid, substantial meal. Now we have it. One of the greatest figures in the whole history of biology receives at last his just due—a worthy biography. And it *is* worthy,

even of so great a man. At the moment the only biography of a scientific man that we can think of as at all to be considered in the class with this great work is Pearson's *Francis Galton*. Dobell's knowledge of protozoa and of biological history, and of their cognate subjects, is simply colossal, both in depth and range. Furthermore the painstaking and enormously laborious care he has taken to verify from the original source every minutest detail touched upon in the book and capable of being verified, is almost without parallel in modern historical work in the field of science. So also is Dobell's modesty about what he has done. One stands humble and abashed before such a monumental example of scientific scholarship.

Antony van Leeuwenhoek was a difficult subject for a biographer. He knew no language but his own, now archaic, brand of Dutch. Furthermore he was neither a "professor" nor a "doctor" but just an honest shopkeeper (dry goods and notions) who had an interest in looking for, and seeing things for himself, and then telling other people who might be interested about what he had seen. He did the telling chiefly by writing long letters to the then newly founded Royal Society of London. These letters were then translated, and edited, and in some part published. The result of this roundabout technique was to leave considerably less than a perfect record of what Leeuwenhoek really said and meant, but, as Dobell shows, few persons since have taken the trouble to study seriously even these inadequate records.

The author had two primary objects in the preparation of this volume: The first to give an adequate English translation of such part of Leeuwenhoek's original writings as bear upon protozoa and bacteria (and incidentally on some other biological matters); the second to give as true and complete an account as possible of the manner of man he was and how he lived his good and useful life. These objects, together with voluminous, detailed, erudite, witty, and humorous comment and annotation along the way, have been superbly accomplished. The volume is beautifully produced. There are 32 photogravure plates besides text figures, and an excellent detailed index.

This is a very great book. No biologist can call himself educated who has not both read and studied it.

HUMAN BIOLOGY

PROBLEMS OF POPULATION. *Being the Report of the Proceedings of the Second General Assembly of the International Union for the Scientific Investigation of Population Problems. Held at the Royal Society of Arts, London, June 15–18, 1931. Published under the direction of the Executive Committee.*

Edited by G. H. L. F. Pitt-Rivers. George Allen and Unwin, London. 15 shillings net. 6 x 9¼; 378; 1932.

This volume of Proceedings contains the full text of all scientific papers presented at the London meeting of the International Union for the Scientific Investigation of Population Problems. The business proceedings, which have already been published in the *Bulletin* of the Union, are not repeated here. The authors of the papers address themselves to many different aspects of the population problem and sometimes obtain different answers to the same question. Thus while Fischer for Germany and Notestein for the United States concur with earlier investigators in finding an inverse relation between social status and fertility, Edin finds that in Swedish cities the relation is changing from inverse to direct. A number of the papers are devoted to the forecasting of population trends. Thus Reed, on the basis of his saturation curve, concludes that, while the proportion of gainfully employed women in the United States is increasing, it will not become as large as that of gainfully employed men, but that "we are tending toward a position where we shall have one gainfully employed female for every three gainfully employed males;" Whelpton, on the basis of projected trends in specific birth and death rates and in net immigration, concludes that the population of the United States will reach a maximum of 144,600,000 in 1970 and will thereafter decline; Dublin views with alarm the decline in the American birth rate; and Baudhuin forecasts a maximum in the Belgian population as early as 1940

and a marked fall after that. Lotka works out mathematically and by means of numerical examples the changes in the birth rate, death rate and age distribution of a population growing according to the logistic law. Hankins concludes that the fall in the birth rate of western peoples is probably due, not to racial senescence, as Gini contends, but in part to birth control and in part to the physiological effect of the rising tempo of social life. Fawcett considers the effect of natural resources and social organization on population density. Gregory points out that "the ultimate effects of the suppression of migration are . . . likely to be more unfavourable to the immigrant than to the emigrant country." Elton deals with the migrations of animal populations. Crew describes his experiments on populations of mice, which show that while the death rate, reproductive rate and fecundity of the population are affected by population density, there are many individuals which endure with ease the conditions of density to which they are exposed. Altogether these papers represent a notable contribution to a subject of great importance to the world. The value of the book is enhanced by an index.

THE ESKIMOS. *Their Environment and Folkways.*

By Edward M. Weyer, Jr. Yale University Press, New Haven. $5.00. 6 x 9¼; xvii + 491; 1932.

The first half of this outstanding treatise on the Eskimo was presented as a doctoral thesis at Yale. The author, a member of the Stoll-McCracken Arctic Expedition in 1928, does not deal with his experiences as an explorer in the far north (not once does the personal pronoun *I* appear) but has compiled a study of the primitive Eskimo as he exists in his natural conditions, and the adjustments he had made to his original environment before outside influences intervened. Many previous explorers have paved the way for this work. The result is a summing up of all available knowledge concerning the specialization of a race which has had to cope with the most difficult of all environments. More widely distributed than any other primitive people (from East Cape, Siberia, to Eastern Greenland and Labrador), the Eskimos number at present roughly 36,000 individuals. In spite of being thinly scattered over so vast an area they exhibit a culture that is "at once broadly uniform in all its subdivisions and distinct in a large measure from every other culture of the world." Second only to "the marvel of their perfect adjustment to their environment is their conformity to the broadly human traits of mankind." The Eskimos' confidence in tradition is tremendous, and they are deeply influenced by their religion, which is closely connected with the affairs of every day life, such as hunting, cooking, eating, and curing disease. Their finest artistic achievement is in the making of masks. This proficiency doubtless developed out of the custom of destroying the masks at the termination of each ceremony.

The author draws heavily on the notes of such dependable observers as Jenness, Birket-Smith, Stefansson, and many others. In each case the reader is referred to the original source. The excellent maps and the table showing the taboos pertaining to game animals increase the usefulness of the book. The work includes a lengthy bibliography and an excellent index.

MAN'S ROUGH ROAD. *Backgrounds and Bearings from Mankind's Experience.*

By A. G. Keller. Frederick A. Stokes Co., New York. $3.00. 6 x 9¼; viii + 450; 1932.

This book is based on the four volume *Science of Society* by Sumner and Keller. It needs no recommendation to the informed reader. To those who have not the time or the opportunity to read the larger work this volume will be most welcome. The main divisions are: Adjustment, maintenance, religion, propagation and gratification. Each of these consists of several chapters. For example, under religion the chapter headings are: The luck element; The spirit-environment; Fetishism; The ghost-cult; Daimonology; Worship and sacrifice; Magic and science; The medicine-man; and Religion in general. Under prop-

agation: Marriage; Preliminaries to wedlock; Wedlock and the status of woman; The dissolution of wedlock, plural and pair-marriage; Posterity and the family. A searching analysis is made of the primitive period, this being, in the author's opinion, the only way to obtain a sound basis upon which to build a science of society. His reasons are that the primitive period covers by far the longest stretch of society; institutions are here in their lowest terms and in process of growth. Furthermore, a more complete picture of the *whole* of social life can be obtained than by a study of history, which yields facts chiefly relating to politics and the "great man."

The book does not present a panacea for our present ills, but

> a point of view from which to scan the institutions by which we live. It stands for the necessity of knowing the anatomy and physiology of society before hanging out a shingle. It promises no immediate results, even from such study. It opposes no programs that represent the best we can do with the knowledge we have. But it calls for the patient effort to develop a pure social science, even if that seems to be a forlorn hope, as a necessary prerequisite to an applied social science.

Since the book is primarily for the general reader rather than the student, neither reference lists nor index are given, but the arrangement of material very closely follows *Science of Society*, where will be found a large bibliography and an index which is highly useful.

AT HOME WITH THE SAVAGE.

By J. H. Driberg. William Morrow and Co., New York. $3.50. $5\frac{1}{4}$ x $8\frac{1}{8}$; x + 267; 1932.

This is a book which all who expect to come in contact with the so-called uncivilized races should read. While the author, who was in service for fifteen years in Uganda and the Sudan, writes more particularly of the African native, what he has to say in general concerning the importance of the understanding of tribal mores will be highly useful to anyone visiting a community of primitive people. The early chapters deal with the general aspects of social anthropology; the latter part with manners, magic and religion, economic life, law, education, etc. The main emphasis throughout the book is on the rigorous training from childhood which the individual receives in all forms of polite intercourse and tribal customs. He is in no sense carefree, but must conform to definite and often elaborate codes of behavior. While 800 words will suffice the average English speaking individual, the savage must frequently master 2,000. The young must be deferential towards their elders. At a communal hunt if a young boy first perceive the lion he must quietly say that a hyena (a harmless animal) is in the vicinity, in order that he may not unduly alarm anyone. On the other hand, should a stranger speak to a child he must first pick up a handful of ashes and rub it on the child's head. To spit in one group is the most formal of salutations. Sex with all its implications is subject to the most precise regulations and tabus. Primitive law, which demands absolute conformity from all members of the community, has a potent weapon in ridicule, public and formalized.

Professor Driberg's plea is for a more human understanding of the savage. The foreigner who ignores the iron-clad institutions of these people will make little progress in his relations with them. Written for the lay reader the book is not without considerable value to the student. Included in the text are 16 plates. There is a brief bibliography, subject index and an index to tribes.

THE PIONEER FRINGE. *Special Publication No. 13.*

By Isaiah Bowman. American Geographical Society, New York. $4.00. $6\frac{3}{4}$ x 10; ix + 361; 1932.

PIONEER SETTLEMENT. *Coöperative Studies by Twenty-Six Authors. Special Publication No. 14.*

American Geographical Society, New York. $5.00. $6\frac{3}{4}$ x 10; vi + 473; 1932.

In *The Pioneer Fringe*, which serves as an introduction to *Pioneer Settlement*, the author gives a general survey of the problems of land settlement. The fact that

pioneering today is a different problem from what it used to be is clearly demonstrated. It involves more than mere acquisition of land; it is necessary to have machinery and tools with which to produce and sell. The pioneer of today aims also at maintaining a higher standard of living than the old pioneer. Part I of this book deals mainly with the general principles, motives, and methods of present day pioneering and the effects of railroads upon it. Part II discusses the regions in which settlers are at present attempting to gain a footing.

In *Pioneer Settlement*, the reader gets a vivid picture of actual present day pioneering, from twenty-six authors, each a specialist and intimately acquainted with some phase of the problems of the region discussed. The book is exciting to anyone in the least interested in population, sociological, and pioneer problems. One sees what the situation actually is in the regions of Western Canada, South America, Manchuria, Africa, New Zealand, and other areas where settlement is taking place. Discussion settles mainly around the agricultural situation. Almost all of the lands now available for pioneering present great difficulties because of their relative infertility.

THE FRENCH RACE: *Theories of Its Origins and Their Social and Political Implications. Prior to the Revolution.*

By Jacques Barzun. Columbia University Press, New York. $4.25. 6 x 8¾; 275; 1932.

An investigation of the writings of the most significant authors who touched upon race conflict and its socio-political ramifications in France before the eighteenth century. The author shows that race origin was far more than an academic question from the sixteenth century to the revolution. The Nordic-Latin-Celtic race theories were back of all the complex problems of government, religion, taxation and social custom. "Class war in all its aspects, interopposition of kings, nobility, clergy and Third Estate employs the ammunitions of race-pride to vindicate its aims and destroy its opponents." The early French nobility held to the theory of a Germanic conquest in the past over the aborigines of the country and to the inheritance of their political rights by the establishment of fiefs by the companions of Charlemagne. The clash between the nobility and the clergy had its origin in this belief. Writings on the subject prior to the fourteenth century are meager and vague but the controversy between the defenders of the Gallo-Roman and the Nordic theories increased as the clash between the nobility and the lower classes developed into warfare. One of the most vigorous of the writers on this subject was Montesquieu. He held to the theory that the Germans were the "fathers" of the French and of their government. On the other hand, Voltaire, while admitting a double conquest of Gaul by the Romans and by the Franks, did not believe in any subsequent racial division or that the Franks contributed a written law (the original Salic Law). The French had no written customs before the end of the reign of Charles VII (1461). The author has put his material in a convenient form for the student. It is carefully documented and indexed. To those biologists interested in race origins it will be a useful source book.

SAMUEL MARSDEN. *A Pioneer of Civilization in the South Seas.*

By S. M. Johnstone. Angus and Robertson, Sydney. 7s. 6d. 4¾ x 7¼; xiii + 256; 1932.

William Dampier landed on the west coast of Australia in 1688. Early in 1770 Cook landed on the southeastern coast at the spot that later became Botany Bay, though he called it Sting Ray Harbour. In August of the same year he formally took possession of the whole country in the name of the King, and called it New South Wales. During the period from 1776 to 1783, it will be recalled that England engaged in a controversy with her American colonies. At the end of the discussion one result was that America was no longer available as a parking place for English convicts. After due deliberation, and the rejection, for climatic reasons, of Africa

as a substitute, it was decided to use Cook's acquisition, New South Wales, for the purpose, and on May 13, 1787 the first batch of convicts (565 ♂ and 192 ♀) set sail from England.

Six years later Samuel Marsden went out to assist the chaplain of the colony and engage in missionary enterprises generally. He was then 29 years old, just ordained, and just married. The rest of his life was spent in Australia and New Zealand, except for visits home. He was a man of powerful personality and had a great influence in shaping the course of events in the early years of the two great British commonwealths of the southern hemisphere.

The student of human biology interested in the problems centering in what has been called the "clash of cultures" will find this book a mine of sound, well documented information. It is well indexed.

CONGORILLA. *Adventures with Pygmies and Gorillas in Africa.*

By Martin Johnson. Brewer, Warren and Putnam, New York. $3.50. 6¼ x 9¼; 281; 1932.

A mystery story could not be more exciting than this account of Mr. and Mrs. Martin Johnson's travels through the Belgian Congo. The pygmies of the Itura Forest become our intimate neighbors; the gorillas at least know man is about and a few become good friends when finally captured. It is interesting to note that the pygmies do not associate a picture as related to themselves in any way. Martin Johnson after having taken yards of film proposed entertaining his friends by evening movies. After it was over one asked: "When do we get paid?" and one wise little man upon being asked why he saw the same film three times replied: "I wanted to find out what you people saw in them." These people have more the minds of children and are childlike in their emotional life, their love being ruled more by friendly affection than passion. They are monogamous and once a wife is selected she is never deserted.

Johnson takes us into gorilla land and by his vivid writing we feel ourselves almost witnesses of probably the finest and most extensive exploring trip ever taken among the largest of apes in existence. It was estimated that there were at least 20,000 gorillas in the Alumbongo Range and this was only one territory. A few gorillas were caught, and this makes an exciting story in itself. Read this book and you will be thrilled, entertained and educated.

ALCOHOL AND MAN. *The Effects of Alcohol on Man in Health and Disease.*

Editor: Haven Emerson. Associate Editors: Henry A. Christian, Reid Hunt, Arthur Hunter, Charles C. Lieb, Walter R. Miles, Ernest G. Stillman. The Macmillan Co., New York. $3.50. 6 x 9¼; xi + 451; 1932.

At first glance this book would seem to be giving the average man who wants to know the real facts concerning alcohol a new deal. It has a distinguished list of editors and collaborators who have tackled the subject with vigor. Should one wish to learn of the effects of alcohol on human functions the first three chapters set forth selected ideas on the subject. The effects of alcohol on the cell and in heredity are rounded up in three more sections. Then alcohol as a poison and a medicine is discussed in the next two sections, the second of these consisting of papers by five physicians. Two chapters are devoted to alcohol and body resistance and pathology; three to the effect of alcohol on man's conduct and mentality; and three to alcohol and longevity, mortality and morbidity, with a final chapter on a review of recent literature on alcohol as a community health problem. By the time all of these various avenues have been traveled by the man "who wants to know" he will find himself emerging from the same old hole at which he entered. Too much alcohol is held to be always bad, no alcohol at all is generally approved of, though occasionally and somewhat grudgingly admitted to be not wholly desirable, and perhaps alcohol in moderate amounts is not always too bad. Each section contains a list of references. Figures and numerous tables explain the statistical data. The volume concludes with a glossary and

author index and a detailed subject index. The aridity of the editor is but ill-concealed.

A History of Ancient Mexico. 1547–1577.

By Fray Bernardino de Sahagun. Translated by Fanny R. Bandelier from the Spanish Version of Carlos Maria de Bustamante. Fisk University Press, Nashville, Tenn. $2.80. 6 x 9; ix + 315; 1932.

To Bernardino de Sahagun, a Franciscan monk, who went to Mexico in 1520 and remained there until his death in 1590, we are indebted for the first ethnological studies of ancient Mexicans. To Mrs. Bandelier, a student of early Spanish, we are indebted for this very able translation of the first part of Sahagun's history of twelve volumes from the Spanish version of Carlos Maria de Bustamante. More is to appear later. After a biographical sketch of the monk the sections of the volume are as follows: Book I, Prologue; The gods which ancient Mexicans adored; Book II, Feasts and sacrifices with which the natives honored their gods in the times of their paganism—Appendix to Book II; Book III, The origin of the gods—Appendix to Book III; and Book IV, About judicial astrology or art of divining which these Mexicans used in order to know which days were lucky and which were unlucky; about the fate of those who were born on days attributed to the marks or signs given below. It appears rather a matter of necromancy than of astrology. Mrs. Bandelier includes a bibliography of de Sahagun's works extracted from *Bibliografia Mexicana del Siglo XVI* by Señor Garcia Icazbalceta (Mexico, 1886). This is to be amplified in her second volume by additional data not now available. The work includes a foreword by Clark Wissler. There is an excellent index.

When the Scot Smiles *in Literature and Life. By A. H. Charteris. Alexander Maclehose and Co., London.* 12s. 6d. 5½ x 8¾; xiii + 304; 1932.

The author, formerly a solicitor in Glasgow, now living in New South Wales, where he is Professor of International Law in the University of Sydney, divides his book into three parts. In the first he analyses the characteristics of Scottish humor and traces it through prose and poetry from the time of William Dunbar (1465–1520) to modern times. As there are differences of character among the Scots due to place of birth, so are there differences of humor. It is all tinged, however, with a grim satire. The reason for this is

> surely to be found in the desperate poverty of Scotland which until long after the Union forbade urbanity, while the constant inculcation of strong moral doctrine—'the eternal verities' of the sage of Ecclefechan —permitted a humorous toying even with sacred things, only possible to those who are safely anchored in the faith.

In the second part of the book the author draws on his own recollections of Scottish humor in the Senate of the University, in the Law Courts, and in the city officers; the third part is from the papers of the late James Hamilton Muir concerning the adventures of "The Nipper" a typical pushing Scottish clerk. The book contains 16 illustrations, some of them very amusing. It is without an index.

Social Anthropology.

By Paul Radin. McGraw-Hill Book Co., New York. $3.50. 5¾ x 9; xii + 432; 1932.

The author of this book is lecturer in anthropology at the University of California. He has written, not for the professional anthropologist, but for "that vast array of students in economics, history, political science, jurisprudence, sociology and psychology who realize the bearing of social anthropology on their subject. . . . " He has kept his discussion free, except in the introductory chapter on the *History of Ethnological Theories*, from all general theoretical problems and has likewise avoided physical anthropology, archeology, linguistics and art. His problem is "the nature and range of primitive man's adjustment to his social needs and to the external world about him. How has he met the problems that have confronted man ever since he came into the world?" The

volume is divided into five main divisions as follows: The organization of the state; the organization of law and custom; the organization of economics and industrial life; religion and ritualism; and literature and mythology. The author does not limit himself to American tribes but uses all primitive peoples as the basis for his treatment. The work includes five maps showing tribe distribution, and a bibliography of 115 titles. It is well indexed.

ETHNOGRAPHICAL SURVEY OF THE MISKITO AND SUMU INDIANS OF HONDURAS AND NICARAGUA. *Smithsonian Institution, Bureau of American Ethnology Bulletin 106.*

By Eduard Conzemius. U. S. Government Printing Office, Washington. 25 cents. 5⅞ x 9; vii + 191; 1932 (paper).

These two related tribes inhabit the larger part of the region known as the Mosquito Coast on the Atlantic side of Honduras and Nicaragua. The population of the Miskito tribe numbers about 15,000 at the present time, that of the Sumu about 3,000; and the author of this bulletin is of the opinion that the day of their complete disappearance or absorption by the Miskito tribe is not far off. Ever since the days of the buccaneers and early settlers the Miskito have assimilated all races, especially the negro, whereas the Sumu have mingled little with foreigners and remain a pure Indian tribe. This bulletin contains a mass of information concerning these two tribes; their physique, government and social organization, households, clothing, occupations, tools, amusements, music, hygiene, religion, marriage customs, burial customs, etc., past and present.

THE GOLD-HEADED CANE.

By William Macmichael. Edited with Explanatory and Illustrative Notes and an Essay on William Macmichael, M.D., His Life, His Works, and His Editors, by Herbert S. Robinson. Froben Press, New York. $3.50. 6 x 9; xxxi + 223; 1932.

The sixth edition of this delightful medico-literary classic, first published in 1827, has been prepared with the intention of giving the reader, besides the original story of the Cane and its five masters, a biographical sketch of the author, William Macmichael; an account of his works, with bibliographical descriptions; specimens of Macmichael's handwriting, and separate portraits of himself, his wife, and their only child. The narrative as written by Macmichael contains many references which this editor has sought to annotate carefully as it is his conviction that

> a reference means little or nothing unless it is explained . . . . and that it is in every way better to find a note that one does not or may not need, than to need a note that one does not find.

Hence the book contains nearly 100 pages of notes and appendices. There is an index.

NIEDERSÄCHSISCHE BAUERN. II. *Bevölkerungsbiologie der Elbinsel Finkenwärder vom dreissigjährigen Krieg bis zur Gegenwart.*

By Walter Scheidt. Gustav Fischer, Jena. 9 marks (paper); 10.50 marks (cloth). 6⅞ x 10¼; vi + 95 + folding table; 1932.

This monograph contains an analysis of biostatistical data found in the parish records of the island of Finkenwärder. The period covered most thoroughly extends from 1660 to 1870. The data consist of fairly complete protocols giving, for each individual who lived on the island during that time, the parentage, date of birth, dates and duration of marriage, number with dates of birth of offspring, occupations, date and cause of death, and other details. Theoretically, such data furnish excellent material for the study of certain problems of human biology and the author strongly recommends that modern statistical offices collect similar data. Practically, however, the labor of making the records is enormous and the results, as is well illustrated in this book, appear scarcely commensurate with the cost.

NEW TYPES OF OLD AMERICANS AT HARVARD *and at Eastern Women's Colleges.*

By Gordon T. Bowles. Harvard University Press, Cambridge. $2.50. 6¼ x 9½; xvi + 144; 1932.

Evidence for the presence of secular time trends of average dimensions of the adult human body continues to be derived from data recorded in the gymnasia and departments of physical education of American colleges. The principal material used in the book at hand consists of thirty different measurements on about 500 fathers and their sons, all of whom attended Harvard University between 1880 and 1917. There is also a similar series of measurements on approximately 500 mothers and daughters all of whom attended Smith, Vassar, Wellesley or Mt. Holyoke colleges. The results of the investigation are confirmatory of the now generally accepted conclusion that young adults in most civilized countries are taller, heavier, and in general larger than their parents of a generation ago. There is a short bibliography; the observational data are summarized by publication of means and standard deviations of frequency distributions. Space is given to correlation diagrams which might have been devoted more effectively to actual correlation tables.

WETTER UND KRANKHEITEN.
By Viktor Baar. Verlag "Ars Medici," Vienna. 3 schilling (paper); 4 schilling (cloth). 6 x 9; 171; 1932.

In an effort to trace the effect of various weather conditions on the onset and course of diseases (chiefly nasal, laryngeal, pulmonary and rheumatic) the author, who is chief city physician in Vienna, kept a daily weather report in addition to a record of the illnesses of his patients, over a period of eight years (1919–1926). Whenever more than three cases of a disease with a similar course occurred within two or three days, he looked on his weather chart to search for a contributory cause. His data, presented in diary form, together with monthly weather charts, take up the main bulk of the book. In an introduction he summarizes the diseases studied by months in which they were most prevalent (or, as in the case of tuberculosis, the months in which most deaths from that disease occurred). There is a short bibliography of German titles.

OUR CHILDREN. *A Handbook for Parents. Edited by Dorothy Canfield Fisher and Sidonie Matsner Gruenberg. Prepared and Sponsored by the Child Study Association of America. Viking Press, New York.* $2.75. 5½ x 8¼; ix + 348; 1932.

A convenient handbook to which parents can turn to find the current thought about problems of child rearing. The twenty-nine contributing experts, all recognized authorities, cover adequately the fields of medical care, psychology, physiology, nutrition and school education. The book divides into four parts: (1) The growth and development of the child; (2) The child in the home; (3) The child in the school; and (4) The child in the outside world. Each chapter is prefaced by a list of typical parental questions which the expert writing the chapter may or may not answer, as in every case he has been allowed complete freedom in developing his subject.

SYLLABUS OF MEDICAL HISTORY.
By Victor Robinson. Froben Press, New York. $1.00. 5⅞ x 9; 110; 1932.

This syllabus, by the author of *The Story of Medicine* and *Pathfinders in Medicine*, consists of specimen questions and answers from his course in medical history, a specimen biographical essay on Duchenne of Boulogne from *Pathfinders in Medicine*, illustrations of primitive and Egyptian medicine, a specimen chronology of goiter, an article on The Photostat and its Value to Students of Medical History, by Charles Perry Fisher, a photostatic reproduction of an early text, and an index. Students in Robinson's course are surely fortunate in having so graphic and inspiring a teacher.

A CENTURY OF PUBLIC HEALTH IN BRITAIN. 1832–1929.
By J. H. Harley Williams. A. and C. Black, London; The Macmillan Co., New York. 7s. 6d. net (England); $2.50 (U. S. A.). 5¼ x 7¾; xv + 314; 1932.

It is recommended that this book be included in the collateral reading of students

of public health and preventive medicine, school medical officers, welfare workers, and all who are attracted by health problems. Beginning with the revolutionary and almost inhuman ideas of Edwin Chadwick the author traces in thoroughly readable fashion the progress of organized efforts to improve the public's health. Separate sections are devoted to antituberculosis work, child life and health, venereal disease control, and smallpox. The book closes with short biographical sketches of the "architects of social medicine," including Edwin Chadwick, John Simon, Florence Nightingale, Francis Galton, and Lord Shaftesbury. There is an adequate index.

MEDICAL ASPECTS OF OLD AGE. *Being a Revised and Enlarged Edition of the Linacre Lecture, 1922.*

By Sir Humphry Rolleston. The Macmillan Co., New York. $3.00. 5⅛ x 7¾; ix + 205; 1932.

The material in this well-known book comprises a critical review of opinions which have prevailed at various times on the nature and cause of old age. This new edition contains much new material, and the discussion is brought up to date. It is a charmingly written, scholarly piece of work. There are indices of subjects and persons, and the book is thoroughly documented.

AMERICAN POPULATION BEFORE THE FEDERAL CENSUS OF 1790.

By Evarts B. Greene and Virginia D. Harrington. Columbia University Press, New York. $3.50. 6 x 9; xxiii + 228; 1932.

This source book brings together in a single volume much material not easily accessible to the student of population. This includes estimates, censuses, and partial enumerations, such as number of militia, polls, taxables, or families, for the thirteen colonies as a whole, and for each state and its local subdivisions. The value of the book is enhanced by a bibliography of twelve pages and an index.

THE ILLEGALLY EMPLOYED MINOR AND THE WORKMEN'S COMPENSATION LAW. *U. S. Department of Labor, Children's Bureau Publication No. 214.*

By Ellen N. Matthews. U. S. Government Printing Office, Washington. 15 cents. 5¾ x 9; v + 225; 1932 (paper).

This inquiry is primarily concerned with the workmen's compensation laws as they affect the illegally employed minor, in two states, Wisconsin and Indiana. In the former the youngster injured while working in industries prohibited to him by law is covered by the state Workmen's Compensation Act, and in addition is entitled to extra compensation based upon his probable earning capacity at his majority. In Indiana he is excluded from the Act but may sue at common law.

HARMONIOUS DEVELOPMENT OF WOMEN'S BODIES.

By Alice Bloch. Translated from the Sixth German Edition by Mathias H. Macherey. Ray Long and Richard R. Smith, New York. $3.00. 7 x 10; x + 136 + 13 pages illustrations; 1932.

A rational attitude towards gymnastics is herein expressed. The purpose of exercise, the author states, is to develop a beautiful and graceful body, hence she cautions one to take time in learning the exercises, and not to overdo. The chapter on posture and breathing exercises is especially sound. There is a section of beautiful illustrations of nude figures, to serve as a guide towards performing the exercises correctly. There is no index.

EMPLOYED BOYS AND GIRLS IN MILWAUKEE. *U. S. Department of Labor, Children's Bureau Publication No. 213.*

By Alice Channing. U. S. Government Printing Office, Washington. 10 cents. 5¾ x 8¾; v + 71; 1932 (paper).

FACTS ABOUT JUVENILE DELINQUENCY. *Its Prevention and Treatment. U. S. Department of Labor, Children's Bureau Publication No. 215.*

U. S. Government Printing Office, Washington. 10 cents. 5⅞ x 9⅛; iv + 44; 1932 (paper).

ZOÖLOGY

PHYSIOLOGY OF THE TEMPERATURE OF BIRDS. *Scientific Publications of the Cleveland Museum of Natural History, Vol. III. Contribution No. 21 from The Baldwin Bird Research Laboratory, Gates Mills, Ohio.*

By S. Prentiss Baldwin and S. Charles Kendeigh. Cleveland Museum of Natural History, Cleveland. $2.20 (paper); $2.85 (cloth). 6¼ x 9¼; x + 196; 1932.

This publication includes experimental studies, carried out under controlled conditions, to determine the factors affecting avian temperature, and studies of the way in which these factors affect the bird under natural conditions. Most of the work was performed on the eastern house wren, *Troglodytes aedon aedon.* The body temperature of birds at standard metabolism, 104.4°F., was used as a basis for comparing the influence of various factors. Among those found to stimulate the amount of heat produced are: emotional excitement, muscular activity, food, extreme changes of air temperature, and attentiveness on the part of the adult female when incubating eggs. The lower and upper lethal limits of body temperature are 71.0°F. and 116.3° F., respectively.

The body temperature of nestling birds, and the temperature of the eggs and nest are also investigated. The temperature of young birds in the nest, before development of a temperature control, varies directly with that of the nest. During the period in the nest there is a gradual rise of body temperature independent of environmental conditions and dependent upon the development of the temperature regulating mechanism. This rise amounts to 0.6°F. per day. Egg temperature under experimental control varies directly and rapidly with air temperature.

A bibliography is included, comprising all the important papers having a direct bearing upon the physiology of temperature in birds, and there is a full index.

WILD LIFE COMMISSION OF MALAYA. *Report of the Wild Life Commission. Volume I —General Survey. Volume II—Recommendations. Vol. III—Malayan Enactments, Extracts from Laws of Other Countries, etc.*

Government Printing Office, Singapore. $4.00 per volume. 6 x 9⅜; Vol. I, 421 + vii; Vol. II, 289 + ix + 29 plates + 2 folding maps; Vol. III, 379; 1932 (paper).

This report of the Wild Life Commission for the Malay States and the Straits Settlements comes at an opportune moment, for there is probably no part of the British empire where less attempt has been made to preserve the native fauna. Up to now, there has been very little protectionist sentiment in that part of the world, and the exploitation of large areas for rubber plantations has resulted in an attitude distinctly hostile to preservation.

Mr. Hubback has made a valuable contribution to the literature of conservation in this report on an area of some 53,000 square miles. Not only does the commission critically examine the present state of affairs, but also offers constructive remedies in the shape of draft enactments complete down to the last detail of game department organization and creation of a self-maintaining game fund. These proposed plans are based on a world-wide knowledge of game laws. It seems to us that any legislative body should be sufficiently impressed by the breadth of technical and practical knowledge displayed to confirm the recommendations of the commission without too much modification. The survey was completed in eight months, in the course of which the two investigators covered some 7,300 miles. The cost of the survey, including printing the report, was $11,000 (a Straits dollar is worth 2/4).

It seems noteworthy that a small, relatively undeveloped country such as Malaya should invest in such a survey of its wild life resources with a view to their preservation and more efficient utilization.

THE VERTEBRAL COLUMNS OF RICOCHETAL RODENTS. *Bulletin of the American Museum of Natural History, Volume LXIII, 1932, Article VI.*

By Robert T. Hatt. American Museum of Natural History, New York. $1.65. 6¼ x 9¾; 139 + 10 plates; 1932 (paper).

Approximately 60 specimens, belonging to

over 40 different genera (8 families), furnish the basis for quantitative and qualitative comparisons of the skeletal characteristics of ricochetal rodents. The introduction contains a concise discussion of related modes of locomotion and the ricochet is defined as

"Forward progression by a series of rebounds in which the two hind feet strike the ground at the same moment and practically synchronously, and the fore feet not at all. This is rapid, sustained hopping." (p. 602). Although it is stated that "ricochetal rodents have their vertebral columns modified from the primitive quadrupedal type more for the changed mechanical conditions consequent to bipedalism and the ricochet, than for other activities," (p. 702).

great variation is introduced by "other activities." Morphological characteristics, which are definitely correlated with the type of locomotion, will require a good deal more study of many more cases than were available for this report. There is a bibliography of 151 titles; ten plates illustrate various characteristics of the ricochetal types; twenty-three pages are devoted to tables which indicate that percentages and ratios are still favorite modes of expressing observational data.

THRILLS OF A NATURALIST'S QUEST.
By Raymond L. Ditmars. The Macmillan Co., New York. $3.50. $5\frac{7}{8}$ x $8\frac{3}{4}$; xii + 268; 1932.

Two features make this book different from most scientists' reminiscences. Ditmars learned to write smoothly and colloquially while working as a reporter, and he learned about snakes in spite of anything anyone could do about it. The former accomplishment has given him the ability to set down his observations about snakes, and himself, in an unaffected way, and the second provided him with the groundwork of his narratives. He collected poisonous snakes as a boy and kept them in his bedroom, not without memorable incident, and studied snakes under natural conditions in both Americas, and in captivity in the zoo and in the circus. Interesting observations on the habits of snakes and of captive animals in general are scattered all through the book. A great many of his activities in collecting, feeding, and transporting snakes to the zoo had to be done surreptitiously and often this resulted in amusing incidents. It strikes us that almost anyone interested in nature, from a twelve year old Girl Scout to an emeritus professor ought to find this an entertaining account of the life and doings of a wide-awake naturalist.

MEDICAL ENTOMOLOGY.
By Robert Matheson. Charles C Thomas, Springfield, Ill. $5.00. $6\frac{1}{4}$ x $9\frac{1}{4}$; xiii + 489; 1932.

This scholarly work opens with a brief historical account of the great leaders in medical entomology. The author then proceeds to discuss the various orders of arthropods and their bearing on human disease. The book is designed essentially as an introduction for the student, physician, public-health man, entomologist and layman. It is written in textbook form and limited in scope, in general, to a classification and description of each insect discussed, its effect on man, its occurrence in nature, and possible means for its extermination. A great deal of sound advice about dealing with insects is given. Each chapter is provided with a selected bibliography.

THE COPEPODS OF THE WOODS HOLE REGION, MASSACHUSETTS. *Smithsonian Institution, United States National Museum Bulletin 158. By Charles B. Wilson. U. S. Government Printing Office, Washington.* 75 cents. $6\frac{1}{4}$ x $9\frac{3}{4}$; xix + 635 + 41 plates; 1932 (paper).

This report, which comprises a study of marine, brackish-water, and fresh-water copepods—free-swimming, commensal, semiparasitic, and parasitic species—is based largely on the collection made by the late Dr. Richard Rathbun from 1881 to 1885, together with collections made by the author. The descriptions pay especial attention to the living coloration of the species. As a result of the use of trawl wings in dredging and of the examination of ponds and sand beaches many species never before reported from the Woods Hole

region have been found. Keys are included as an aid in identification; the keys to the genera include practically every valid genus thus far described; the keys to the species include only those found in the region. There are bibliographic references to the species and an index.

ECONOMIC MAMMALOGY.

By Junius Henderson and Elberta L. Craig. Charles C Thomas, Springfield, Ill. $4.50 postpaid. $6\frac{3}{8}$ x $9\frac{1}{2}$; x + 397; 1932.

Since the literature on economic mammalogy has been scattered extensively through a large number of periodicals, an attempt to condense this information into a book is justified. The book is well written in the textbook form and should be a useful introduction for students. Among the subjects considered are the economic relations of mammals; their direct and indirect influence on humanity; their food habits; methods of preserving and increasing those species of use and benefit to man, and the control of harmful mammals. There is an extensive bibliography and an index.

FOODS OF SOME PREDATORY FUR-BEARING ANIMALS IN MICHIGAN. *University of Michigan, School of Forestry and Conservation Bulletin No. 1.*

By Ned Dearborn. University of Michigan Press, Ann Arbor. 25 cents. 6 x 9; 52; 1932 (paper).

The results of an investigation on the food habits of the raccoon, opossum, red fox, coyote, wild cat, skunk, mink, weasel and badger, based on examinations of stomach contents and residues in the feces.

MY SWANS. *The Wylly-Wyllys and Others. By E. L. Turner. J. W. Arrowsmith, London.* 3s. 6d. $5\frac{1}{2}$ x $7\frac{1}{8}$; 126; 1932.

We find comparatively few people interested in these beautiful birds and seldom any possessing such intimate knowledge of their thought and life as our author. The illustrations are splendid, the account is short and attractively written.

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung XXII.*

Edited by G. Grimpe and E. Wagler. Akademische Verlagsgesellschaft, Leipzig. 13.60 marks. 6 x $8\frac{1}{2}$; 152; 1932 (paper).

In this installment of an excellent survey of the fauna of the North and Baltic seas, previous numbers of which have been reviewed in these columns, the following groups are dealt with: Archiannelida, by A. Remane; Phoronidea, by Carl I. Cori; Euphausiacea, by C. Zimmer; Cetacea, by L. Freund. Each section is furnished with a bibliography.

REMARKS ON THE AFFINITIES OF THE MAMMALIAN FAUNA OF VANCOUVER ISLAND, BRITISH COLUMBIA, WITH DESCRIPTIONS OF NEW SUBSPECIES. *University of California Publications in Zoology, Volume 38, No. 12.*

By E. Raymond Hall. University of California Press, Berkeley. 25 cents. $7\frac{1}{8}$ x $10\frac{3}{4}$; 11; 1932 (paper).

BOTANY

WILD FLOWERS OF THE ALLEGHANIES. *Being a Description of Their Character, Habits, Flowering Season, and Location; a Concise Definition of Colors, References to Medicinal Properties, Notations of the Insects that Assist in Their Fertilization; also Numerous Flower Legends, Historical References and a Fully Illustrated Key to the Most Important Diagnostic Characters of the Families Represented. A Check List of Ferns Occurring in the Area is Appended.*

By Joseph E. Harned. Joseph E. Harned, Oakland, Md. $4.50. $5\frac{3}{8}$ x 8; xxxii + 670; 1931.

FLOWERS OF GRASS. *How to Know the Names of the British Grasses. A Handbook for Beginners.*

By Robert Fisher. Wheldon and Wesley, London. 2 shillings. 5 x $7\frac{1}{4}$; 47 + 11 plates; 1932.

There is no reason why more botanical manuals of the type of *Wild Flowers of the Alleghanies* should not be written for nature lovers and for beginners to whom the standard taxonomic books are appalling. Harned's book is a thoroughly respectable

key to the ferns and flowering plants of the Alleghany Mountains from Canada to the northern part of Alabama written by a man who takes pleasure in studying nature. It is beautifully illustrated with large and accurate drawings, colored plates, and a few first-rate photographs, but it is not in any sense the usual picture-book kind of flower manual. It aims to tell something about plants besides their names; bits of mythology from antiquity and folklore from the Americas; the kind of remarks an observant field naturalist would set down; and whatever features of plants struck the author's fancy. He is not only religious, but devout, there is no mistaking that. In spite of that we are bound to admit that he seems to have the knack of teaching science to young people, and to amateurs in general, as few people have.

The manual of the British grasses is intended for beginning botanists, and as this is by no means an easy group of plants to study, it has nearly 30 illustrations designed to show the structure of grasses and their flowers. Perhaps the illustrations and the studied simplicity of the analytical key should make it useful to American amateur botanists as a supplement to the usual taxonomic manuals, as many species are common to the British Isles and to the region covered by Gray's Manual.

MEN OF THE TREES. *In the Mahogany Forests of Kenya and Nigeria.*

By Richard St. Barbe Baker. The Dial Press, New York. $5.00. $6\frac{1}{4}$ x $9\frac{1}{8}$; 283; 1931.

The material for this book stems from the author's experience as Assistant Conservator of Forests in Kenya and Nigeria. In spite of the fact that it is replete with the kind of enthusiastic uplifting goodness that would be expected to trickle stickily from a pot in which Pollyanna and a Boy Scout had been boiled down together, the book does contain a considerable amount of useful and interesting information, and a lot of superb photographs. Both the ecologist and the anthropologist will find material in it. Tropical forests are shown not to be inexhaustible. The wrong kind of exploitation can easily wipe them out. The author's chief missionary concern is to insert this idea into the native's head, and at the same time teach him how to manage his forests so that hopefully he will still have the kind of dwelling place to which he is attached, even after the white man has taken his loot from the green gold of the forest. Apparently he has been rather successful in this enterprise. The book has no index.

ROOT NODULE BACTERIA AND LEGUMINOUS PLANTS. *University of Wisconsin Studies in Science Number 5.*

By Edwin B. Fred, Ira L. Baldwin, Elizabeth McCoy. University of Wisconsin, Madison. $3.00. $7\frac{5}{8}$ x $10\frac{5}{8}$; xxii + 343; 1932 (paper).

This is a well written critical review of the literature on the symbiotic bacteria associated with leguminous plants. Root nodules were first figured by Fuchs in 1542 and since then a great amount has been written on several phases of the problem. The subject as it is treated here should be of interest to several kinds of scientific workers. Bacteriologists will find a considerable portion of the monograph devoted to the cultural characteristics of the bacteria and their relation to nitrogen in the plant and on culture media. The treatment of the development and histology of nodules of bacterial origin in leguminous plants and in a few other species falls within the range of interest of botanists, as should also three or four pages on some plants whose nodules are in the leaves. Agronomists will find a good deal of space devoted to methods of inoculation and to the economics of the method. There are nearly fifty full page plates, judiciously chosen, numerous tables, an index, and more than a thousand bibliographical citations, to supplement the text.

CONTRIBUTION À L'ÉTUDE ÉCOLOGIQUE DES BLÉS DE LA REGION DU RHONE MOYEN (DRÔME-ARDÈCHE).

By A. Dusseau. Office Régional Agricole du Midi, Marseille. 6 x $9\frac{1}{2}$; 214; 1932 (paper).

Throughout France the baking quality of wheat depends in high degree upon the locality in which it is grown, but fortunately for the French farmer the tastes in bread vary just as much, and almost every grade of wheat is specially esteemed somewhere. This variation has prompted a taxonomic study of wheat varieties on a biometric basis, the ecological conditions under which they are grown, and the quality of flour they yield. Mlle. Dusseau's report on the Puy-de-Dôme was reviewed in an earlier issue of THE QUARTERLY REVIEW OF BIOLOGY; this bulletin concerns the departments Drôme and Ardèche. In these papers, which are in large part summaries of official statistics, she has been able to leave the charts showing soil types and distributions of arable lands and crop yields relatively free from unneeded lettering by the simple device of providing maps printed on celluloid bearing the names of cantons and rivers which may be superimposed on the charts.

DER FORMWECHSEL DER PENNATEN DIATOMEEN (KIESELALGEN).

By Lothar Geitler. Gustav Fischer, Jena. 20 marks. 6¼ x 9; 226; 1932 (paper).

Diatoms have an interesting life cycle

which begins with the auxospore, continues in the vegetative division of the cells with progressive reduction in size and is terminated by the production of auxospore mother cells and auxospores which is generally connected with sexuality. Small cells in which auxospore production is suppressed continue to divide with progressive reduction in size until a certain minimal size is reached. Such cells cannot re-enter the developmental cycle but die off.

In the normal life cycle, diminution in size is accompanied by alterations in the proportions of the cells, for the most part due to a lessening of the relative length of the apical axis. This alteration in form has been traced through the developmental cycles of a number of diatom species. The bibliography has more than 150 titles.

SOME ASPECTS OF PLANT NUTRITION.

By B. Viswa Nath. Society of Biological Chemists, Bangalore, India. Re. 1. 5½ x 8½; 39; 1932 (paper).

This little review begins with the remark that "between the years 2500 B.C. and 500 A.D. the knowledge of soils and plants possessed by ancient India was at a high standard of level, approaching modern views and practices in many respects. For ten centuries after the year 500 A.D. the trail of progress of agriculture is lost." In order to bring Indian agronomists up to date again in knowledge of soil management Mr. Nath has prepared a very good review of about 150 papers on soil science and plant physiology, emphasizing the interrelationships of soil, plants, and animals. Unlike American experiment station bulletins, this ends on a philosophic level with a passage on the essential unity of life and the balance of Nature.

RESPIRATION IN PLANTS.

By Walter Stiles and William Leach. The Dial Press, New York. $1.50. 4⅛ x 6½; vii + 124; 1932.

The purpose of this book is to give "an account of the nature of plant respiration which is readable and understandable by the elementary student of botany and which at the same time contains sufficient information to render it of value to the advanced student." Both kinds of students, and physiologists in general, will find this a very useful survey of a heterogeneous subject in which the experimental work is of very uneven quality. The method is to discuss a limited number of researches that illustrate the more important principles of plant respiration, closing with a chapter on recent theories of the chemical mechanism of respiration. There is a bibliography of about 120 titles and a usable index.

ALCOHOLIC FERMENTATION.

By Arthur Harden. Longmans, Green and Co., New York. $5.50. 6 x 9⅝; vii + 243; 1932.

This is the fourth edition of a standard monograph on the mode of action of the enzymes concerned in the fermentation of sugars by yeast. It does not consider the physiology of the growing yeast cell at

any length but is confined for the most part to the properties of the yeast juices and the chemical changes they induce. There is a very well written historical introduction, covering 17 pages. Compared with the third edition the number of citations has been nearly doubled and amounts to a little less than a thousand. It is provided with an excellent index.

MORPHOLOGY

LEHRBUCH DER HISTOLOGIE UND HISTOGENESE. *Dritte, Neubearbeitete Auflage.*

By Josef Schaffer. Wilhelm Engelmann, Leipzig. 18 marks (paper); 20 marks (cloth). $6\frac{5}{8}$ x $9\frac{3}{4}$; viii + 576; 1933.

Part I of this excellent text treats of the simple tissues; Part II of the histology of organs and glands. The second edition was published ten years ago and the author has revised it page by page to bring this third edition up-to-date. The embryonic development of the lattice fibres, supporting tissues, the construction of the neuroglia, the smooth muscle fibres of the alveoli of the lungs, and the placenta are treated in greater detail. The section on glands has been entirely rewritten, and the physiological and biological aspects as well as the morphological are discussed. A bibliography of 26 pages has been added. An adequate index, over 600 excellent text figures, and 14 colored plates further enhance the value of this book, which is altogether an outstanding textbook.

A MANUAL OF EMBRYOLOGY. *The Development of the Human Body.*

By J. Ernest Frazer. William Wood & Co., Baltimore. $8.00 net. $6\frac{1}{4}$ x $9\frac{1}{4}$; viii + 486; 1932.

The regional method is employed in this book in describing the development of the human embryo. The subject is dealt with in two parts. In Part I, the early and general development of the embryo is considered, and in Part II, the development of organs and regions. New descriptions, derived by the author in working out on human material the processes of development, are incorporated. No references are included, except that when a statement is made on the authority of some other worker the name is put in brackets. There is a full index.

GRUNDZÜGE DER ENTWICKLUNGSGESCHICHTE DES MENSCHEN IN VERGLEICHENDER DARSTELLUNG. 13., *neubearbeitete Auflage.*

By Richard Weissenberg. Georg Thieme, Leipzig. 13.50 marks. 5 x $7\frac{3}{4}$; xviii + 448 + 5 plates; 1933.

In addition to having undergone another revision as to text—notably in the sections on the development of the circulatory system of the liver and the development of the brain—this standard handbook of embryology has been considerably dressed up as to format. This edition is printed on a high-grade quality of paper which enhances the text figures, and a number of new figures have been added or substituted.

PHYSIOLOGY AND PATHOLOGY

THE MECHANISM OF NERVOUS ACTION. *Electrical Studies of the Neurone.*

By E. D. Adrian. University of Pennsylvania Press, Philadelphia. $2.00. 6 x 9; x + 103; 1932.

This work is primarily concerned with the behavior of the units which make up the nervous system, as determined with the aid of the vacuum tube amplifier. The best results, to date, have come from the peripheral nerves. When a nerve is stimulated electrically, it is found that the potential change in each fibre is of fixed magnitude and duration, and that it depends only on the state of the fibre and not on the strength of the stimulus which set it in motion. The activity of the sensory nerve fibres in transmitting messages to the central nervous system seems to consist merely of a series of brief impulses or waves following one another more or less closely. In any one fibre the waves are all of the same form. The same kind of electrical activity is found in the motor nerve fibres. The impulses in the sympathetic system and in the smallest sensory fibres are conducted much more slowly than those in the

large motor and sensory fibres, but there is no evidence that any other kind of activity is present than that involved in the conduction of impulses. The same kind of activity is found in nerve fibres from all sorts of animals.

The action of the sense organs is then considered. Variations in excitability and in adaptation rate are the chief differences which can be observed in the reactions of the sense organs which respond to mechanical stimulation. The work of Wever and Bray on the auditory nerve is discussed, and the conclusion drawn that with the auditory as with the tactile nerve fibres the intensity of the stimulus is judged by the number of impulses making up each volley.

A chapter is devoted to the pain mechanism. The main problem is that of the specific effects of different sensory fibres. Increase of stimulus is known to cause more intense pain. The question arises as to whether pain is due to a very high frequency of discharge, or whether it is due to nerve fibres which can give rise to no other sensation. From data obtained from work on the frog and on mammals it is concluded that it is unlikely that pain is always due to specific pain fibres.

It may be nearer the mark to say that the sensation produced by nerve fibres of a given type becomes a closer and closer approach to pure pain in proportion to the slowness of conduction of the fibre and the lack of sensitivity in the end organ. The most sensitive tactile endings and their rapid nerve fibres cannot cause pain: the slow non-medullated fibres with their endings which respond only to noxious stimuli can cause little else, but for all we know the smaller medullated fibres may give both contact or pain according to the magnitude of the discharge.

Discharges in motor fibres are then considered, and in the final chapter, the activity of nerve cells. In closing, the author states:

All conclusions about the central nervous system must be tentative, and the conclusion of this work is little more than a restatement of the cellular hypothesis. The nervous system is built up out of specialised cells whose reactions do not differ fundamentally from one another or from the reactions of the other kinds of excitable cell. They have a fairly simple mechanism when we treat them as individuals: their behaviour in the mass may be quite another story, but this is for future work to decide.

The book contains a bibliography and is indexed.

HEARING IN MAN AND ANIMALS.

By R. T. Beatty. G. Bell and Sons, London. 12 shillings net. $5\frac{1}{2}$ x $8\frac{3}{4}$; xi + 227; 1932.

A fascinating description of the nature of the various mechanisms by which animals, from insect to man, hear, and the evolution of these mechanisms. The book is primarily designed for the general reader, but it will also be instructive to biologists unfamiliar with its specialized field. The author has collected and correlated data from the fields of anatomy, physiology, physics, acoustic engineering and psychology and has written down this information with as little use of technical terms as possible.

The first chapter, which gives a detailed description of the human ear and the functions of its various parts, is followed by a discussion of the evolution of the ear, beginning with the primitive auditory mechanisms of fishes. A chapter each is devoted to the resonance and non-resonance theories of hearing. The chapter devoted to hearing in animals contains some interesting facts and explodes some time-honored beliefs. Fish, we learn, cannot hear air-borne sounds, so the fisherman need no longer heed Isaac Walton's advice, but may talk to his heart's content without fear of lessening his catch. Snakes, likewise, are insusceptible to air-borne sounds, and react to the charmer's motions rather than to his piping. Other material is concerned with brain and nerve mechanisms involved in the process of hearing; music; noises; and defects in hearing. References are listed at the end of each chapter, and an index has been provided.

SOME FACTORS IN THE LOCALISATION OF DISEASE IN THE BODY.

By Harold Burrows. William Wood & Co., Baltimore. $4.50. $5\frac{3}{8}$ x $8\frac{1}{2}$; xi + 299; 1932.

This book is divided into three parts. Part I deals with localisation from the bloodstream of colloidal and other matters and includes chapters on the localisation of normal and foreign proteins, of dyes and fine inorganic particles, of syphi-

lis, bacteria, viruses and cancer. In Part II factors in localisation are considered. Part III is devoted to a general discussion of the phenomenon of localisation. The conclusion is that

> Three conditions are required for the localisation of many blood-borne diseases—namely:
> (1) An abnormal permeability of the walls of the small blood vessels.
> (2) The presence of forces which will transport the noxious agents through the endothelial cytoplasm.
> (3) The retention of noxious agents in the tissues under the influence of inflammation.
> The three conditions mentioned above lead to the localisation, not only of the agents of disease, but to the factors of defence.

There is a full bibliography and an index.

FADS AND QUACKERY IN HEALING. *An Analysis of the Foibles of the Healing Cults, with Essays on Various Other Peculiar Notions in the Health Field.*

By Morris Fishbein. Covici, Friede, New York. $3.50. 5½ x 8½; vii + 384; 1932.

The thing that distinguishes this book from most protests against medical quacks and fraudulent health treatments is that Doctor Fishbein's indignation is usually mixed with amusement, not malicious humor or irony, but a good-natured appreciation of the ridiculous. For instance, after dealing with chiropractic according to its deserts he is able to say

> Most of the patients of chiropractors are women. An old farmer down in Kansas said that he had noticed that whenever a man came to a chiropractor, the bone in his spine that was out of place was usually near the head. The idea offers intriguing possibilities for continued thought.

This sort of thing not only makes interesting reading, and there is page after page of it, but it impresses us as being an uncommonly good means of combatting the quacks. Christian Science, osteopathy, the Abrams box, and a host of health cults with fancy names, come in for some rough treatment, along with muscle builders and beauticians; in fact, in one sense it is an annotated catalogue of the more conspicuous individuals or groups who have competed or interfered with scientific medicine in this country since colonial times. It has a useful index.

A GUIDE TO HUMAN PARASITOLOGY *for Medical Practitioners.*

By D. B. Blacklock and T. Southwell. William Wood and Co., Baltimore. $4.00 net. 5⅞ x 9⅜; viii + 271; 1932.

This book is intended for the practitioner who has had no experience in parasitology. Emphasis is laid only on the pathogenic organisms, and descriptions are restricted to those characters in them which are of immediate diagnostic value. The technique of using a microscope and of examining material is outlined, after which the parasites are systematically described. Eleven tables deal with the relation of parasites to food and water, different vehicles in the spread of parasitic diseases, the diagnostic features of parasites, and other matters. Mention is made of some of the drugs of use in the treatment of the different diseases. A list of larger text books is given and there is an index.

PROTOPLASMIC ACTION AND NERVOUS ACTION. *Second Edition.*

By Ralph S. Lillie. University of Chicago Press, Chicago. $3.00. 5 x 7½; xiii + 417; 1932.

The subject matter of this book, widely and favorably known in its first edition, is concerned with the fundamental biological problems of vital organization, growth and development.

> The structural and physico-chemical organization of living matter, the modifiability of its rate of reaction under varying conditions (irritability), and its transmissive property (so highly developed in nervous tissues) are considered in some detail; and their probable relation to the polyphasic and film-partitioned character of the protoplasmic system is indicated.

Previous experimental work in the field is summarized and the author's own studies are included. The book is well documented, and there is an index. The changes and additions in the second edition are not great, and are only for the purpose of bringing the discussion up to date.

PHYSIOLOGY OF FARM ANIMALS.

By F. H. A. Marshall and E. T. Halnan. The Macmillan Co., New York. $3.25. 5½ x 8⅝; xiv + 366; 1932.

A book which covers successfully a field of physiology hitherto neglected, and certainly of economic importance. There is a great deal of valuable information for the stock breeder, though the book is written primarily as a textbook for students of agriculture. The first part of the book, after a brief discussion of histology and chemistry of foods, devotes a chapter to each of the organ systems. The last part gives a survey of present knowledge of the growth and nutrition of farm animals.

VISION AND COLOUR VISION.

By R. A. Houstoun. Longmans, Green and Co., New York. $4.50. 5⅜ x 8½; vii + 238; 1932.

An extensive discussion of vision from the physical, physiological, and psychological standpoints, with rather more emphasis on the physical side. The author, however, deals with the multiplicity of factors concerned in the phenomenon of color vision in a logical and thoroughly sound manner. The book embodies the most recent work on vision, most of which has not yet been put into the textbooks. There is an interesting discussion of the Young-Helmholtz theory of color vision, pointing out some of its logical weaknesses.

A TEXTBOOK OF GENERAL PHYSIOLOGY *for Colleges.*

By Philip H. Mitchell. McGraw-Hill Book Co., New York. $6.00. 5⅞ x 9; xviii + 799; 1932.

This is the second edition of an excellent general physiology textbook designed for students whose training in physical chemistry and biochemistry is meager.

In addition to the general revision, the second edition differs radically from the first in two respects:

1. Much less space has been given to the biochemical aspects of physiology in order to make room for more physical chemistry as applied to physiology. To this end, several of the earlier chapters have been eliminated or condensed and four entirely new ones, Surface Action, The Colloidal State, Diffusion and Osmosis, and The Permeability of Cells, have been added.

2. The general arrangement of the subject matter as indicated by the new order of chapters has been changed to conform with what seems to be the more general and convenient practice among teachers of general physiology.

VETERINARY PATHOLOGY AND BACTERIOLOGY.

By S. H. Gaiger and Gwilym O. Davies. Alex. Eger, Chicago. $6.50. 5⅜ x 8⅜; viii + 610; 1932.

The outstanding feature of this textbook is its photographic illustrations, mostly from original specimens in the Museum of the Department of Animal Pathology in the University of Liverpool. These are numerous and excellent. The text is organized on a subject basis. Pathology, bacteriology, virus infections, protozoology and mycology as found in animal diseases are concisely but well treated. This is a sound and useful text, well indexed.

THE PRINCIPLES OF OPTICS.

By Arthur C. Hardy and Fred H. Perrin. McGraw-Hill Book Co., New York. $6.00. 5¾ x 9; xiii + 632; 1932.

This textbook of optics ought to be welcomed by biologists because of the care taken to describe the kinds of optical equipment which find application in biological work, and to discuss the principles of their operation. The chapters on light sources, photography, light-sensitive cells, and microscopes, should be particularly useful to biologists. There are numerous references to more technical treatments of particular topics, and there is an excellent index.

RECHERCHES SUR L'INFECTION, L'HYPERSENSIBILITÉ ET L'IMMUNITÉ *vis-à-vis des Formes Virulentes ou Atténuées du Virus Tuberculeux.*

By Jean van Beneden. Masson et Cie, Paris. 25 francs. 5½ x 8⅞; 135; 1932 (paper).

A description of important experiments conducted by the author in the Laboratories of Bacteriology and Hygiene of the University of Liège, bearing on the filtrable element of the tubercular virus and on the attenuated stock of Calmette and Guérin

(BCG). The purpose was to differentiate diverse reactions of infections, hypersensibility to tuberculin, hypersensibility to superinfection, and immunity. The author believes that the differences which these experiments have established between certain reactions will facilitate an understanding of the close connection between various phenomena concerned in the acquisition of resistance to tubercular infection. The book is equipped with a bibliography on BCG and ultra-virus, and an author index.

INTRODUCTION À LA CHIRURGIE NERVEUSE. *By E. E. Lauwers. Masson et Cie, Paris.* 25 francs. $6\frac{1}{4}$ x $9\frac{1}{4}$; vii + 121; 1932 (paper).

A résumé, written primarily for the use of the neural surgeon, of the important researches made in recent years concerning the physiology and pathology of the nervous system. The various chapters treat of the meninges and the cerebrospinal fluid, encephalon, spinal marrow, peripheral nerves, and the sympathetic nervous system. The book lacks an index and a systematic bibliography, although some references—a total of 82—are given as footnotes.

HEALTH DEPARTMENTS OF STATES AND PROVINCES OF THE UNITED STATES AND CANADA. *Public Health Bulletin No. 184 (Revised). Compiled by John A. Ferrell, Wilson G. Smillie, Platt W. Covington, Pauline A. Mead. U. S. Government Printing Office, Washington.* 75 cents. $5\frac{3}{4}$ x $9\frac{1}{8}$; vi + 785; 1932 (paper).

An extensive and useful summary of official public health organizations in each of the states and provinces of the United States and Canada. The compilation is thoroughly done and furnishes a valuable source for reference.

CANCER AND SARCOMA ONE; IDENTICAL IN CYTOLOGY. *Finding the Pure Cancer Cytology, Only, in a Reported Case of Undifferentiated Round Cell Sarcoma; Revision of Many Cases of Sarcoma Yield Pure Carcinoma on Restudy. Does "Cure of Cancer" 10–18 Years, Post Operation with no Recurrences, Then Fatal Recurrences, Suggest a Dormant Abeyant Chronic Form of Cancer—a Benign Form of Cancer? Various (30) Cases in Point of Discussion. The Causal Diminutive Cancer Cellulettes, Dormant or Active, Must be Neutralized or Destroyed for Ultimate Cure. A Further Amplification of the Specific Cancer Cellule and Its Conduct. Transmutation. Cell Division. By Frank A. Stahl. Frank A. Stahl, Hamilton Club, Chicago.* Edition limited complimentary. 6 x $9\frac{1}{8}$; 60; 1932 (paper).

BIOCHEMISTRY

ON THE MECHANISM OF OXIDATION. *By Heinrich Wieland. Yale University Press, New Haven.* $2.50. $5\frac{7}{8}$ x $9\frac{1}{8}$; x + 121; 1932.

Wieland has set forth in this book his concept of the mechanism of biochemical oxidations and has supported it with evidence drawn from general chemistry and from his own experiments on acetic acid and fermentation and the Schardinger enzyme of milk. The basis of his well known scheme is that oxidation is effected by a transfer of hydrogen from the substance undergoing oxidation, or its hydrate, to a hydrogen acceptor which is thereby reduced, and he has assembled some very interesting sets of data which accord with this hypothesis. An alternative means of accounting for oxidation involves the catalytic activity of iron and about a quarter of the book is devoted to this topic. There is an index and a small bibliography.

MODERN ALCHEMY. *By William Albert Noyes and W. Albert Noyes, Jr. Charles C Thomas, Springfield, Ill.* $3.00 postpaid. $5\frac{5}{8}$ x $8\frac{7}{8}$; ix + 207; 1932.

"The vicissitudes of the search for transmutation and for healing principles are typical of the progress of science and have been taken as the ground work of this book," say the authors in their preface.

The result is a somewhat superficial survey of a wide variety of subjects ranging from cosmogony to hormones and vitamins. This book must appeal chiefly to the general scientific reader; there are brief and simple explanations of the latest theories of the constitution of matter, the new quantum mechanics, valence, and methods for healing and control of disease. For the benefit of those whose interest is stimulated to further and more profound reading on these subjects there is a list of bibliographical references at the end of each chapter. There is an index.

MEDIZINISCHE KOLLOIDLEHRE. *Lieferungen* 1, 2, 3.

Edited by L. Lichtwitz, Raph. Ed. Liesegang and Karl Spiro. Theodor Steinkopff, Dresden. 5 marks per number. 7½ x 10¼; Lief. 1, 80; Lief. 2, 72; Lief. 3, 80; 1932–1933 (paper).

This series when completed will consist of some 10 *Lieferungen*. These first three numbers treat of general theories of colloids with reference to biology and pathology. The following papers are included: Introduction, with sections on protoplasm, aging, assimilation and storage, by R. E. Liesegang; Colloidal-osmotic pressure of biological fluids, by Paul Meyer; Surface tension (capillary electricity and growth), by F. Herčik; Permeability (membranes, theory of adhesive pressure, electric potentials, and thixotropy), by F. Leuthardt; Formation of concretions, by L. Lichtwitz and K. G. Stern; Immunity, by A. Klopstock; and Enzymatic action, by K. G. Stern. Later numbers will discuss the application of colloid research in medicine, and technique.

THE CHEMICAL INVESTIGATION OF PLANTS. *By L. Rosenthaler. Authorised Translation of the Third, Improved and Enlarged German Edition by Sudhamoy Ghosh. G. Bell and Sons, London.* 12s. 6d. net. 5½ x 8½; viii + 197; 1930.

This book is intended to provide an introduction not only to the working methods of plant biochemistry but to the logical processes of forming judgments on the suitability of various procedures; which is to say, the subject is treated in somewhat more general terms than in the usual cookbook type of analytical manual. The emphasis is upon quantitative methods throughout. It is meant to be a guide to research in pharmacology and agricultural chemistry, and accordingly there is a useful bibliography of works on special fields. The book opens with a short chapter on the history of the subject—something of a novelty—and closes with a good index.

PH AND ITS PRACTICAL APPLICATION. *By Frank LaMotte, William R. Kenny and Allen B. Reed. The Williams & Wilkins Co., Baltimore.* $3.50. 6 x 9; vii + 262; 1932.

This manual is intended for the use of laboratory assistants and technicians in the numerous industrial processes and routine laboratory procedures in which pH measurements find application. The elementary principles of these measurements are explained, and the uses they find in a dozen industries are discussed in separate chapters. A very useful feature of the book is its charts showing typical pH values encountered in practice. There are chapters; on bacteriological and clinical laboratory methods and on soils. There are bibliographies at the end of each chapter and an index.

BIBLIOGRAPHICAL SURVEY OF VITAMINS 1650–1930. *Compiled by Ella M. Salmonsen. With a Section on Patents by Mark H. Wodlinger. Mark H. Wodlinger, 86 East Randolph St., Chicago.* $10 net. 6⅞ x 10; v + 334; 1932.

This excellent bibliography contains approximately 12,000 references in chronological order, covering both foreign and domestic publications, from 1650 to 1930. The bulk of the references occurs after 1916. After that date they are subdivided by type of vitamin. Not only will this bibliography be enormously useful to students working in its particular field, but it also furnishes fine material for statistical

studies of the sort made by F. J. Cole on the literature of comparative anatomy, and E. Wyndham Hulme in broader fields.

PHYSICAL CHEMISTRY FOR STUDENTS OF BIOLOGY AND MEDICINE.

By David I. Hitchcock. Charles C Thomas, Springfield, Ill. $2.75. 5½ x 9; xi + 182; 1932.

The material in this book has been offered during the past five years to medical graduate students in Yale University as a part of the course in physiology. The topics which have been selected from the whole field of physical chemistry are those especially pertinent to biological work, and most essential to an appreciation of modern research. The subject-matter is presented with directness and clarity. There is a bibliography of 96 titles and an index.

PRÉCIS DE CHIMIE PHYSIOLOGIQUE. *Onzième Édition.*

By Maurice Arthus. Revised and brought up to date in collaboration with André Arthus. Masson et Cie, Paris. 65 francs. 4¾ x 7½; xii + 522 + 5 plates; 1932.

The eleventh edition of a standard work, first published in 1895. Some theories which have proved to be unsound in the light of present day knowledge have been omitted, and considerable new material has been added to bring the book up-to-date.

SEX

SEX AND INTERNAL SECRETIONS. *A Survey of Recent Research.*

Edited by Edgar Allen. The Williams & Wilkins Co., Baltimore. $10.00. 6 x 9; xxii + 951; 1932.

An excellent symposium by twenty-two authorities on the most important recent research in the problems of sex endocrinology, a subject which has had such a rapid growth within the last few years that the research has not been properly evaluated or generally appreciated, and for that reason a survey is greatly to be welcomed.

After a general biological introduction by F. R. Lillie, there are two chapters devoted to a comprehensive discussion of the genetics of sex as found (a) generally in animals, particularly birds and mammals, by C. H. Danforth, and (b) in *Drosophila*, by C. B. Bridges. Embryological foundations of sex in vertebrates are discussed by B. H. Willier, which leads directly to an interesting chapter on sex deviations and the general theories of intersexuality by E. Witschi. The remaining fourteen chapters treat in great detail the physiology of the gonads and the influence of endocrine factors on them as these factors have appeared and been established from laboratory investigations. Riddle contributes an account of the metabolism of sex. The biology of the testes is discussed at length by C. R. Moore, who divides his account into a discussion of testicular activity in the non-mammalian vertebrates and the mammalian, devoting considerable space in the latter section to the factors influencing spermatogenesis. The biochemistry of the testes is summarized by F. C. Koch. The ovarian follicular hormone, theelin, and the biochemistry of this hormone, the physiology of the corpus luteum, and the mammary glands, are discussed with admirable thoroughness in four chapters by E. Allen, E. A. Doisy, F. L. Hisaw, and C. W. Turner. C. G. Hartman gives an interesting account of the recent theories of the mechanism of ovulation, with a description of his own work on the Carnegie monkey colony. Effects of implants of the anterior hypophysis (P. E. Smith) and effects of extracts of the anterior pituitary (E. T. Engle) as well as anterior pituitary changes referable to the reproductive hormones, and the influence of the thyroid and the adrenals on genital function, by A. E. Severinghaus and the two preceding authors, adequately dispose of the pituitary, at present the most popular endocrine gland. There is an important chapter on plumage tests in birds, by L. V. Domm, Mary Juhn and R. G. Gustavson. The last two chapters deal with the subjects of sexual drive (C. P. Stone), and endocrine disorders in sex function in man (J. P. Pratt), which are necessarily treated more generally than the preceding sections owing

to the greater difficulties involved in experimental work along these lines.

Each author reviews critically the work that has been done in the particular subject he is discussing, and points out where the weaknesses lie, and what directions future research may profitably take. Those interested in the progress of sex research will find this book of great value.

THE RHYTHM OF STERILITY AND FERTILITY IN WOMEN. *A Discussion of the Physiological, Practical, and Ethical Aspects of the Discoveries of Drs. K. Ogino (Japan) and H. Knaus (Austria) Regarding the Periods When Conception Is Impossible and When Possible.* *By Leo J. Latz. Latz Foundation, Chicago.* $1.00. 4 x 6; vii + 108; 1932.

This book is written in the question and answer method. To quote from the publisher's (and author's) blurb its central thought is: "Women are sterile (cannot conceive) during about three-fourths of the menstrual cycle. The discoveries of Drs. K. Ogino (Japan) and H. Knaus (Austria), which show how the periods of sterility and fertility can be determined, are explained in a popular style." We might add, also in a somewhat sentimental style. By way of illustration we quote questions 14, 55 and 64.

14. What is menstruation?

If the mother cell does not find her 'hero' she languishes and dies within a few hours. She is carried down the Fallopian tube to the uterus, where everything is in readiness to receive a living guest—not a dead mother cell.

The *corpus luteum*, not receiving any information, stops its activities, withers, and decays. The pituitary gland is free to exert its influence. The muscles of the womb again begin to contract and expand, and by so doing expel all the special preparations that were stored up. Blood and mucous substance leave the womb. This phenomenon is called menstruation.

55. What is contraception?

Contraception is the deliberate use of some artificial means (such as voluntary interruption, chemical or mechanical devices), in order to prevent the father cell from meeting the mother cell, in other words, to prevent conception. It means, then, interfering directly with the workings of nature in the marital act.

64. But does periodic abstinence not seem opposed to God's holy will as expressed in the command "Increase and multiply and fill the earth" (Gen. 1, 28)?

If the literal meaning of these words is stressed too much, every person reaching puberty would have to enter the married state, vows of chastity would have to be abrogated, married people would not be allowed to observe continence and would be obliged to bring into the world a maximum number of children. This evidently cannot be the meaning of the text, nor can it be the will of God.

Our Catholic friends are apparently leaning more heavily upon this treatise in their anti-birth control propaganda than its merits warrant. There may be a dependable "safe period" in the reproductive cycle of the human female, but if there is that fact will be established by physiological rather than biblical research, we opine.

THE PRACTICE OF BIRTH CONTROL. *An Analysis of the Birth-Control Experiences of Nine Hundred Women.* *By Enid Charles. Williams and Norgate, London.* 10s. 6d. net. 5½ x 8½; 190; 1932.

This book is devoted to the analysis and discussion of data regarding the prevalence and effectiveness of contraceptive methods as used in England. The material used is derived from three sources. The first is from questionnaires sent out by the Birth Control Investigation Committee of England; the second from questionnaires collected by Nurse Daniels from persons who had been supplied and fitted by her with Dutch caps; the third from the records of the Birmingham Women's Welfare Center (a birth control clinic). From the first source 432 cases were available for analysis; from the second, 198; from the third, 244. Out of the total number of women in the three series (874) there were exactly 12 –(p. 23) who had never used any contraceptive method whatever, available for comparison with women who had used some method or other. This is admittedly an inadequate control. The author is, therefore, of necessity, thrown back upon making comparisons between different contraceptives.

A great variety of other questions are, however, discussed statistically and otherwise in the volume. Indeed the diffuseness of the treatment, and a readiness to base discussions of very broad and complex problems of fertility upon material that fails to satisfy some of the simplest canons

of sound scientific methodology, leaves an unfortunate impression regarding an obviously sincere, honest, and laborious undertaking. The book will, however, be useful for purposes of comparison to other students in the same field, within its limitations. It is refreshingly free from propaganda. And in so difficult and complicated a field as that of human reproduction in its relation to population problems any contribution, however modest, is welcome.

THE SEX TECHNIQUE IN MARRIAGE.
By Isabel E. Hutton. Emerson Books, New York. $2.00. 5 x 7½; 160; 1932.

THE HYGIENE OF MARRIAGE. *A Detailed Consideration of Sex and Marriage.*
By Millard S. Everett. The Vanguard Press, New York. $2.50. 5½ x 8; 248; 1932.

The first book, with its four pages of laudatory press opinions, will no doubt continue to find favor among those persons, both medical and lay, who believe that a superficial knowledge of the anatomy and physiology of sex, mixed with pious admonitions, will help to solve the difficult problems of sex in marriage.

Professor Everett, although not himself medically trained, has written a more comprehensive, a less dogmatic, and withal a better book. The last four chapters under the headings: the need for birth control, birth control laws, birth control clinics, and scientific versus hearsay methods of contraception, are particularly well done and give the information desired by most people who seek out and read such books.

PARENTS AND SEX EDUCATION. *For Parents of Young Children.*
By B. C. Gruenberg. Viking Press, New York. $1.00. 5⅛ x 7⅝; viii + 112; 1932.

The problem, which all parents face, of how and what to teach their children about sex, is approached in this book from a thoroughly realistic point of view. The author recommends as a first step the adoption of a matter-of-fact point of view toward the whole question of sex by the parent. Suggestions based on sound child psychology and characterized by definiteness are then outlined for meeting the situations most commonly arising, and for forestalling undesirable situations. The final chapter presents supplementary biological information for parents. The treatment throughout is practical and unsentimental.

BIRTH CONTROL.
By Johann Ferch. Translated with a Biographical Foreword by Christian Roland. Edited, with an Introduction, by A. Maude Royden. 3s. 6d. *Rider and Co., London.* 4¾ x 7⅝; 124; 1932.

In this book the founder of the Austrian League for the Protection of Mothers discusses the ethics of birth control and the methods of contraception used by the League. No method, he admits, is able to prevent impregnation with absolute certainty. As an interim measure until the knowledge of birth control is more widely disseminated and more certain methods are discovered he also advocates the legalization of abortion during the first three months. On the latter point Maude Royden and the translator do not agree with him.

MAN AND WOMAN IN MARRIAGE.
By C. B. S. Evans. Bruce-Roberts, Chicago. $2.00. 4¾ x 7⅛; 113; 1932.

This little book is one of the clearest and most sensible expositions of the *ars amandi* that we have seen in some time. The importance of the wife's reaching an orgasm and the technique of insuring that result are emphasized. There is no bibliography or index.

BIOMETRY

STATISTICAL METHODS FOR RESEARCH WORKERS. *Fourth Edition—Revised and Enlarged.*
By R. A. Fisher. Oliver and Boyd, Edinburgh and London; G. E. Stechert and Co., New York. 15 shillings net (Great Bri-

tain); $4.00 (U. S. A.). 5½ x 8¾; xiii + 307 + 7 folding sheets of tables; 1932. That this book has reached a fourth edition in seven years speaks well for its usefulness. The principal additions to this edition deal with the analysis of covariance. The appendix to the chapter on frequency distributions has been rewritten to include the *k*-statistics and cumulants, "since the inconveniences of the moment notation seem now definitely to outweigh the advantages formerly conferred by its familiarity." There are a bibliography and an index.

As to the Method of Maximum Likelihood, which forms the corner-stone of Fisher's statistical philosophy, we are still uncertain whether it is more than a verbal evasion of the difficulties of inverse probability. However, the only alternative to some such method seems to be inductive agnosticism; we are, therefore, disposed to accept it in practice, while entering a caveat as to its theoretical foundation.

ELEMENTARY MATHEMATICS FROM AN ADVANCED STANDPOINT. *Arithmetic. Algebra. Analysis.*

By Felix Klein. Translated from the Third German Edition by E. R. Hedrick and C. A. Noble. The Macmillan Co., New York. $3.00. 6⅛ x 9¼; ix + 274; 1932.

Besides his important mathematical researches Klein was interested in the teaching of mathematics, not only in the universities, but in the secondary schools. The lectures which he gave for many years to secondary school teachers of mathematics were finally printed, and the present volume is a translation of Part I of this work. Among the points which Klein emphasizes in the teaching of mathematics are the importance of the function concept, the mutual connection between problems in various fields, the necessity in elementary and secondary instruction of a concrete and intuitional approach to mathematical concepts, and the value of a historical treatment of the development of mathematics. There are numerous bibliographical references in the text and an index.

PSYCHOLOGY AND BEHAVIOR

DEVELOPMENT OF AN INFANT CHIMPANZEE DURING HER FIRST YEAR. *Comparative Psychology Monographs Vol. 9, No. 1, Serial No. 41.*

By Carlyle F. and Marion M. Jacobsen and Joseph G. Yoshioka. Johns Hopkins Press, Baltimore. $1.50. 6⅞ x 10; 94; 1932 (paper).

In this paper Carlyle and Marion Jacobsen contribute the introduction and the section on behavioral development, and Joseph G. Yoshioka the section on physical growth and physiological maturation. There is a foreword by Robert M. Yerkes. The parents of this baby chimpanzee (Alpha, born 246 days after conception) were well known as to their psychobiological characteristics, having been under close observation for several years previous to the birth of their offspring. They had only just come into sexual maturity. Since the mother refused to care for the baby the investigators were able to rear her in isolation from her kind for many months and to obtain a unique and important series of observations covering many phases of her growth and development. Comparing the chimpanzee records for the first seven months with records of human infants for an equal period the graph shows that

> In creeping, sitting and walking the chimpanzee infant is increasingly accelerated over healthy human infants; that the chimpanzee is also accelerated in skeletal development, the arms more so than the legs; and that the extent of the behavioral acceleration approximates closely that of the skeletal.

Concerning the relatively simple tests of eye-hand coördination Alpha was equal to or slightly accelerated over the human child. In imitation Alpha failed completely in the first year, and succeeded in passing only the simplest items in the second year. Comparing Alpha's behavior tests with those of the human infant, the investigators note the following points:

> Although the chimpanzee passed many test items at the lower age levels, toward the end of the year she had reached a point beyond which she made but little progress. The absence of language did not appear to be the immediate cause of such failure since

numerous non-language tests involving imitation and exploitive behavior were failed. Examination of Alpha in the second year, and incidental observations on older chimpanzees, have indicated that within marked limits the chimpanzee is capable of performing additional test items but only after greater experience and development. Among the test items which were passed, the temporal sequence in which they were accomplished followed rather closely the order for the human infant.

In the majority of test situations other than postural and locomotor development the chimpanzee tended to maintain about the same age level as the average human child. The volume includes tables and charts exhibiting growth rates, etc.; an appendix in which is given the responses to Gesell normative items; a brief bibliography; an index and a series of plates showing Alpha in infancy.

REMEMBERING. *A Study in Experimental and Social Psychology.*

By F. C. Bartlett. The Macmillan Co., New York. $5.00. 6⅛ x 9½; x + 317; 1932.

A book for the student and experimentalist rather than for the general reader. The work had its origin in an investigation to determine the different factors (and their functions) involved in the course of normal visual perception. It was necessary to extend the study to related mental processes and in particular to a study of imagery and recall. While the work was mainly in individual perceiving, imagery and remembering, it included also experiments with social groups as units. The investigator adopted a strictly functional point of view:

> All considerations of the descriptive characteristics of *what* is perceived, imaged or remembered have been kept in a secondary position. The central problems all the time have been concerned with the *conditions*, and the variety of conditions, under which perceiving, imaging and remembering take place.

The first 227 pages of the book present the experimental work. "Remembering," the author states in the chapter devoted to his theory, "is not re-excitation of innumerable fixed, lifeless and fragmentary traces."

> It is an imaginative reconstruction, or construction, built out of the relation of our attitude towards a whole active mass of organised past reactions or experience, and to a little outstanding detail which commonly appears in image or in language form. It is thus hardly ever really exact, even in the most rudimentary cases of rote recapitulation, and it is not at all important that it should be so. The attitude is literally an effect of the organism's capacity to turn round upon its own 'schemata,' and is directly a function of consciousness.

The latter part of the book is concerned with the study of specific social influences upon remembering such as social psychology, social psychology and the matter and the manner of recall, conventionalisation, the notion of a collective unconscious, and the basis of social recall. While the author occasionally refers the reader to the work of other investigators, he includes no literature list. The work contains a few figures and plates and is indexed.

THE PHYSICAL MECHANISM OF THE HUMAN MIND.

By A. C. Douglas. The Williams & Wilkins Co., Baltimore. $4.00. 5⅜ x 8½; xiv + 251; 1932.

The problems of presenting a theory of mind in such a way that both the intelligent general reader and the specialist in psychology will be interested presents numerous difficulties. That is what the author of this book has attempted to do. That he has succeeded in his project those readers who belong in the first class will agree. The specialist will no doubt find flaws, but even so will admit that the book merits his attention. More than one sitting will be required by the layman to master the book. In spite of the clear and logical manner of presentation the substance is far too meaty to be digested rapidly. In the preface the author briefly outlines the two main currents of thought which lead up to *Associationism* and the recent trend towards *Behaviorism* in America and *Gestaltism* in Germany. Then he states the aim of the present work:

> I believe, and I hope to demonstrate, that by taking full advantage of the latest advances in physiological knowledge the gaps left by Associationism may be filled, the criticisms and requirements of Gestaltism may be met, and a complete scientific theory of Mind may be presented, upon the materialistic basis which Behaviourism rightly demands.

Up to Chapter X such subjects are discussed as the principles of nerve arrangement and nerve action in the higher vertebrates and man, the elements of psychoneural correlation, the mechanism of space-time perception and habit, instinct and motion. It is clearly brought out that the phases of mind so interlock and interpenetrate that in order to understand one the whole field must be arrayed. The latter part of the book (pages 144 to 244) is concerned with the construction of his theory. The work includes figures and diagrams, a bibliography of 33 titles, a brief list of books on psychology for the general reader, and an index.

THE USE OF THE SELF. *Its Conscious Direction in Relation to Diagnosis, Functioning and the Control of Reaction.*

By F. Matthias Alexander. E. P. Dutton and Co., New York. $2.00. 5⅛ x 7½; xix + 143; 1932.

Doctor Dewey in an introduction enthusiastically endorses Mr. Alexander's methods of central and conscious control. He says:

> If there can be developed a technique which will enable individuals really to secure the right use of themselves, then the factor upon which depends the final use of all other forms of energy will be brought under control. Mr. Alexander has evolved this technique.

In the first part of the book the author describes in detail his experiment by means of which he was able to correct faulty habits in speaking and reciting. He discovered that

> my sensory appreciation (feeling) of the use of my mechanisms was so untrustworthy that it led me to react by means of a use of myself which *felt* right, but was, in fact, too often wrong for my purpose.

Lengthy experience as a teacher verified this belief in the prevalance of sensory untrustworthiness and its significance in the problem of the control of human reaction. Separate chapters deal with the problems of the stutterer and of the golfer who cannot keep his eye on the ball. In the final section on diagnosis and medical training emphasis is placed on the importance to the physician of a training in the satisfactory direction of the use of his own mechanism. This would enable him

> to judge the manner of use present in the patient, detect any misdirection of use, and, when this exists, determine its relation to any symptoms of unsatisfactory functioning present.

The book is indexed.

HABITS. *Their Making and Unmaking.*

By Knight Dunlap. Liveright, New York. $3.00. 5¾ x 8⅝; x + 326; 1932.

The purpose of this volume is "to outline the interrelation of the processes of learning and unlearning, of habit making and habit breaking," and in an elementary way "to show how a fuller understanding of the learning process makes possible more adequate procedure in the breaking of disadvantageous habits."

Dunlap in his discussion of the psychology of learning has abandoned the conventional method to be found in so many text books for a position which in many instances seems almost revolutionary. He by no means claims that his interpretations are final. That he has succeeding in casting aside many of the false premises which have so long befogged psychological studies and established a sounder, more rational basis for future work his book amply testifies. The headings of the 12 chapters are as follows: The problems of habit and learning; The fundamental principles of learning; Voluntary and involuntary action; Physiological theories of learning; The process in learning; The conditions of efficient learning; Retaining, recalling and relearning; Remembering and forgetting; Personal and social adjustment; The breaking of specific bad habits; Habits of emotional response; Learning ability and intelligence. The work is not too formidable for the lay reader although the last four chapters dealing with practical application will undoubtedly receive his closest attention. There is a bibliography and an index.

A STUDY OF ERROR. *A Summary and Evaluation of Methods Used in Six Years of Study of the Scholastic Aptitude Test of the College Entrance Examination Board.*

By Carl C. Brigham. College Entrance Examination Board, New York. $5.00. 8½ x 11; xiii + 384; 1932.

The first two chapters of this book are theoretical. Chapter I consists almost entirely of excerpts from the writings of Titchener and Dewey whose antithetical points of view, the one psychological, the other societal, are contrasted. Spearman is found to occupy both positions. The use of symbols as a means of communication between individuals is discussed in Chapter II. The author offers the following definition of the science of education:

> that science which regards experience as dependent upon a pluralism of communicating individuals. The subject-matter of this science, formally considered, is societal, and, materially considered, is symbolic.

In analyzing the results of the Scholastic Aptitude Tests the methods of correlation and partial correlation are used. The tests themselves fall into five groupings: synonyms, analogies, antonyms, double definitions and paragraph reading. The intercorrelations between these tests are very high.

The remainder of the book is devoted to methods of treating symbols objectively. Chapter III presents an experiment in using pictorial instead of verbal material in the test composition. In the following chapters the various tests are studied intensively for significance and reliability. It is interesting to note that each type of test material showed approximately identical solutions when repeated on a population similarly sampled. Separate chapters are devoted to evaluations of the arithmetic tests and the spatial relations tests. The appendices include a description of the administration of the tests, and the six annual reports (1926–1931) of the College Entrance Examination Board.

STUDIES IN CONCEPT FORMATION. *I. The Development of the Concept of Triangularity by the White Rat. Comparative Psychology Monographs, Vol. 9, No. 2, Serial No. 42.*

By Paul E. Fields. The Johns Hopkins Press, Baltimore. $1.25. 6⅞ x 10; 70; 1932 (paper).

This volume presents evidence to support the theory that each individual (infrahuman included) has evolved his own concepts and that there must be a period during which the concept is developed, in contradistinction to the theory that concepts are peculiar to man and are present in him ready-made. Specifically, the purpose of this paper is to determine, granted that a white rat is able to discriminate an equilateral triangle (apex up) from a circle of equal area and brightness, whether this discrimination is based upon the rat's recognition of the qualities of triangularity as opposed to the qualities of circularity, or whether the discrimination merely results from the reaction of the rat to a differential retinal distribution of light without any reference to the qualities inherent in such distributions. Eleven white rats were given a total of over 40,000 trials to 80 different stimulus cards which were presented in more than 240 combinations. The conclusion drawn from the data which were obtained is that

> when white rats are given a training period specifically designed to provide a large number of different "triangle experiences," the rats are able to perfect a type of behavior which is fully described by the implications inherent in our use of the term "concept."

THE MEDICAL VALUE OF PSYCHOANALYSIS. *By Franz Alexander. W. W. Norton and Co., New York.* $2.75. 5¼ x 8; 247; 1932.

This book is a simple, straightforward account of the psychoanalytic doctrine. The subject-matter is treated as a science and not as a dogma, an accomplishment which is the more commendable because it is so rare. The significance of psychoanalysis for medicine is seen in the following two accomplishments:

> 1. With the help of a technique specifically adapted to the nature of psychic phenomena, it has developed a consistent and empirically founded theory of the personality, fit to serve as a basis for the understanding and treatment of mental disturbances. 2. It has given a concrete content to the philosophic postulate that living beings are psychobiological entities, by investigating in detail the interrelation of physiological and psychological processes. The greater part of these investigations must, however, be left to the future for completion.

The second chapter, in which the author describes the present status of psychoanaly-

sis as a theory and as a therapeutical system, is especially interesting. The intimate relation of the therapeutic concepts to the general theory is emphasized. The contents of this chapter are restricted to the concepts which are most essential and empirically best founded.

In chapter III the psychoanalytic treatment of psychoses is critically considered. Chapter IV is devoted to a discussion of psychogenic factors in organic diseases, and the final chapter considers the place of psychoanalysis in medical education. The book is well indexed.

SCHLAF UND TRAUM.
By Hans Winterstein. Julius Springer, Berlin. 4.80 marks. $4\frac{5}{8}$ x $7\frac{1}{4}$; 135; 1932.

DIE WELT DER SINNE. *Eine gemeinverständliche Einführung in die Sinnesphysiologie.*
By W. v. Buddenbrock. Julius Springer, Berlin. 4.80 marks. $4\frac{5}{8}$ x $7\frac{1}{4}$; vi + 182; 1932.

These two books form Volumes 18 and 19, respectively, of the *Verständliche Wissenschaft* series, a series of scientific treatises planned with the general reader in mind. Several numbers have already been noticed in this REVIEW.

The first of the two noticed here is a very readable exposition of the physiological, pathological and psychological aspects of sleep and dreams. The section on the Freudian theory of dreams seems to us fair enough, though Winterstein does not swallow it whole.

Buddenbrock describes in an interesting manner the five senses, broadly speaking, plus the senses of temperature, gravity, and proprioceptive stimulations, their presence, or absence, the various mechanisms involved and their mode of functioning in various organisms from microscopic animals to man. It would make an excellent text for supplementary reading in a scientific German course.

Both of these books are illustrated and the first is furnished with an index.

MOTIVATION OF YOUNG CHILDREN. *An Experimental Study of the Influence of Certain Types of External Incentives Upon the Performance of a Task. University of Iowa Studies. Studies in Child Welfare, Volume V, Number 3.*
By Lucile Chase. University of Iowa, Iowa City. $1.00 (paper); $1.35 (cloth). 6 x $9\frac{1}{4}$; 119; 1932.

This volume presents an experimental investigation of the influence of external incentives upon the performance of tasks done by young children. The study was made on 213 children ranging from two to eight years in age. They were divided into four groups, one serving as a control. In testing the children the motivation-dynamometer, an apparatus devised by the author, was used. The relative effectiveness of repeating directions only between trials, of giving praise between trials, and of giving rewards is determined by comparing the test scores of the groups. The scores were lowest in the first case and highest in the last. The children were tested again, this time for the relative effectiveness of repeating directions only between trials, giving reproof, and giving punishment. The scores in the last two cases show no significant difference, but the differences between the scores of each of the last two cases and the first approach significance. In all of the tests, the control group, receiving only control-motivation, scored lower than the experimental groups receiving any one of the three types of incentive. A bibliography of 57 titles is given.

LYING AND ITS DETECTION. *A Study of Deception and Deception Tests.*
By John A. Larson, in collaboration with George W. Haney and Leonarde Keller. University of Chicago Press, Chicago. $5.00. 6 x 9; xxii + 453; [1932].

The book has much of the fascination that a good detective story has, besides containing an accumulation of carefully criticized literature on the subject. Each type of deception is described and classified; ancient and modern methods used by the police and other officers to deal with criminals are reviewed and shown

to be weak and inadequate. The physical and emotional disturbances concomitant with lying are discussed at length, and there is an interesting section on modern scientific technique in handling criminals. The most valuable part of the book is the final section in which the author gives an outline of his own researches in developing a test instrument (cardio-pneumo-psychograph) to detect emotional responses in individuals. While not perfect this method when combined with others will undoubtedly give valuable additional means for detecting a criminal.

DESIRE AND CREATION.

By K. W. Monsarrat. Henry Young and Sons, Liverpool. 5 shillings net (postage 5 pence). 5⅜ x 8½; 104; 1932.

The author cannot reconcile the trend towards progress with the concept of natural selection and random variation in the individual. He therefore produces a new theory, which is

> that if a living organism corresponds with the unfamiliar and this correspondence is followed by adaptation, a change that has permanence may arise from its own act and may be transmitted to a succeeding generation.

Also, he states that the animate is distinguished from the inanimate, in that it can direct its energy towards work and ultimately creation. Whatever case the author may be trying to make is considerably weakened in the last three chapters, where he writes with a certain lyrical mysticism about the "desire to give" as the greatest thing in life. There is neither index nor bibliography.

CHILD PSYCHOLOGY.

By Buford J. Johnson. Charles C Thomas, Springfield, Ill. $4.00. 6 x 9; xii + 439; 1932.

There is a great deal in this book that is excellent. The subject-matter both covers the literature and presents new studies made in the Child Institute of the Johns Hopkins University. As indicated by the chapter headings, among the points analyzed are the following: infant responses, locomotion, manipulation, speech, thought, emotion, social behavior and personality, and individual differences. No especially new conclusions emerge and no new hypothesis is presented. The book is primarily didactic. It is unfortunate that the use of complex verbiage often obscures the real meaning of a sentence, a criticism which applies to many academic psychologists' presentation of otherwise excellent material. The book contains a bibliography of 206 titles. There are author and subject indices.

MAN AS PSYCHOLOGY SEES HIM.

By Edward S. Robinson. The Macmillan Co., New York. $2.50. 5½ x 7¾; 376; 1932.

For the layman who is more familiar with the lingo than with the actual content of present-day psychological theory and points of view, this book provides an excellent medium for orientation. The subject-matter is presented in two parts. The first part, *Man, comments on his nature*, discusses motivation, the heredity vs. environment controversy, the mechanism of the learning process, man as a functioning personality, and the mind-body controversy. The point of view is detached and practical. The presentation is clear and humorous. Part II, *Psychology, its aims, its deeds, its follies*, is especially interesting in its swift, unbiased survey of psychological methodology, precepts and trends. There is a bibliography and an index.

THE STORY OF SCIENTIFIC PSYCHOLOGY.

By Adelbert Ford. Sears Publishing Co., New York. $3.00. 5½ x 8⅛; xii + 307; 1932.

The general reader and especially those who struggled through the maze of Psychology I in the late Victorian Era, will find this an interesting and informing book. Professor Ford, of Lehigh University, has done *Scientific Psychology* somewhat in the manner of Paul deKruif's *Microbe Hunters*. In his preface he says:

I have written this book to present something of the dramatic history of the science of psychology, showing the peculiar part played by the personalities of research men, the sacrifices made to achieve pure scientific truth, and the nature of some of the findings made in the process of attaining predictability in a subject which was for years in the hands of the mystics.

AN EXPERIMENTAL STUDY OF SUPERSTITIONS AND OTHER UNFOUNDED BELIEFS *as Related to Certain Units of General Science.*

By Otis W. Caldwell and Gerhard E. Lundeen. Bureau of Publications, Teachers College, Columbia University, New York. $1.25. 6 x 9; 138; 1932 (paper).

When discussions of commonly accepted unfounded beliefs, such as that red hair is a sign of violent temper or that lightning never strikes twice in the same place, were incorporated in high school general science class work, a larger proportion of the pupils gave conventionally correct responses in a test than had done so before the discussion. The authors admit that

It would be more desirable to measure changes in attitudes by a study of reactions individuals make when faced with life situations which may influence behavior by belief in unfounded ideas. An adequate technique for measuring attitudes in this way has not been devised.

LES TROUBLES DU SOMMEIL. *Hypersomnies, Insomnies, Parasomnies.*

By Henri Roger. Masson et Cie, Paris. 20 francs. $5\frac{1}{2}$ x $7\frac{3}{4}$; 206; 1932 (paper).

A detailed study of insomnias, hypersomnias, and parasomnias and their causes, together with a critical discussion of therapeutic treatments used in overcoming them. There is a subject index but no bibliography.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE PHILOSOPHY OF PHYSICAL REALISM.

By Roy W. Sellars. The Macmillan Co., New York. $4.00. $5\frac{3}{4}$ x $8\frac{5}{8}$; xiv + 487; 1932.

In this book the author of *Critical Realism* develops his philosophy further. According to this the mind is not imprisoned within its own walls, as Berkeley and his followers had taught, nor, on the other hand, does it literally reach out and touch the stars, as the neo-realists contended. Through meanings founded on sense data the mind gains approximate knowledge of external things. "It is the pattern of things that we can decipher, even though we cannot apprehend the stuff of being."

He rejects the belief in universals "as a peculiar kind of entity in external things which may be in many things at once and gives them an identity of nature." The members of a class are not identical but similar in some respect, and on the basis of this similarity the mind thinks them in terms of the same predicate. It is a matter of logical, not of ontological, identity.

Space, as the extendedness of physical systems, and time, as change or eventness, are accepted by the author. The theory of relativity, he concludes, is a theory of measurement and of the operational interpretation of numbers attached to magnitudes and does not have the ontological significance sometimes ascribed to it.

And I am conservative enough to defend the category of substance against both idealist and eventist. Yet I do not defend a Lockian parody of it. It stands for primary and secondary continuants which are spatial and the *locus* of events and which appear in scientific *description* as space-time worms. There is no inert core to which entities called properties are attached. It is the concrete continuant which we know in terms of what is disclosable about it, which we call its characteristics and executive properties.

As to causality he rejects Russell's attempt to reduce it to regular sequence or uniformity.

Consciousness is for him a quality of brain-events and therefore "as spatial as the brain of which they are events." Finally, valuing is as objective in reference as knowing, but judges an object with respect to human living.

The lover of ingenious paradoxes will, no doubt, find this book pedestrian. To this the author would probably retort that the lover of paradoxes is not the best judge of a system of philosophy.

THE NATURAL SCIENCES. *An Introduction to the Scientific Philosophy of To-day.*

By Bernhard Bavink. Translated from the Fourth German Edition with Additional Notes and Bibliography for English Readers, by H. Stafford Hatfield. The Century Co., New York. $7.50. 6 x 9; xiii + 683; 1932.

Bavink is more concerned about the processes by which one arrives at scientific knowledge than he is about specific results. He appears at his best in the first half of the book, which is devoted to physics and cosmology, fields in which he is most at home. He expounds the newer concepts of these subjects with a clearness and a plausibility that is often absent from such discussions. The other half, titled "Matter and Life" and "Nature and Man," is material more familiar to biologists; these sections should be most useful to interested laymen. Bavink's biology is mostly *Entwicklungsmechanik*, genetics, and evolution, and he deals with its problems as philosophers are wont to do. Mechanism and vitalism, determinism and teleology, the problem of consciousness, and the inheritance of acquired characteristics are all given an airing. In matters of science and religion he takes a conciliatory position. In fact, one of the curious features of the book is the utter earnestness with which he considers such topics as astrology, telepathy, and spiritualism; while he comes to the same conclusions that most scientific men reach he apparently found it harder to convince himself than is usual.

SCIENCE AND SUPERSTITION IN THE EIGHTEENTH CENTURY. *A Study of the Treatment of Science in Two Encyclopedias of* 1725–1750. *Chambers' Cyclopedia: London* (1728). *Zedler's Universal Lexicon: Leipzig* (1732–1750).

By Philip Shorr. Columbia University Press, New York. $1.50. $5\frac{7}{8}$ x $8\frac{3}{4}$; 82; 1932.

In that system of conventional generalizations which passes for history with most of us the eighteenth century is labeled an Era of Enlightenment, in which superstition had given way to science. But in the human mind mutually contradictory ideas can live together more or less peacefully. There is no sharp break between cultural periods: old superstitions can continue to exist side by side with new sciences. Some years ago Lynn Thorndike showed that in Diderot's famous *Encyclopédie* there were abundant remains of earlier superstitions. In this interesting book the author extends the analysis to two other eighteenth century encyclopedias and finds in them a still greater survival of unfounded beliefs. Thus in Chambers' *Cyclopedia* "The great objectives of alchemy are enumerated without a shadow of scepticism" and Galen's remedy for hydrophobia, "to feed the patient a spoonful of ashes of either crawfish or river lobsters twice a day for forty days," is given as an infallible cure. In short, the eighteenth century was still much more an age of transition than we are accustomed to realize.